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TITLE STUDIES ON THE ROLE OF THE MAMMALIAN EXTERNAL EAR IN DIRECTIONAL HEARING.

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STUDIES ON THE ROLE OF THE MAMMALIAN EXTERNAL EAR IN DIRECTIONAL HEARING.

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ABSTRACT

Studies on the role of the mammalian external ear in directional hearing.

D.M.Gower.

The acoustical properties of the external ears of rabbits, rats and guinea pigs have been investigated by means of microphone or probe implants in the ear canal or tympanic bulla and by cochlear microphonic (CM) recordings. The directional properties and transfer functions of the external ears were monitored using pure tones and broad-band sound under anechoic conditions. Broad-band signals were analysed with a high resolution signal analyser. This facilitated the collection of detailed transfer function, interaural intensity difference (IID) and CM spectra over a range of azimuths and elevations under normal and modified pinna conditions. Experimental modifications of the pinna included blocking the fossa, ear canal and tragal notch, removal of the pinna flange and pinna, and modifications to the tympanic membrane.

The on-axis gain in the transfer function of the rabbit ear was shown to be largely the result of the concha whereas in the rat the pinna flange makes a large contribution. Gain from the ear canal appears to be insubstantial in both species. In the guinea pig, the combined effects of the tympanic bulla and ear canal result in substantial gain in the 2kHz-3kHz range. Concha gain is maximal at about 8kHz and pinna flange gain occurs over a wide frequency range.

Transfer function directional sensitivity is greatest in the rabbit at low frequencies. Transfer functions in the rat show relatively low levels of directional sensitivity but over an extended high frequency range, while those of the guinea pig show directional sensitivity at middle and high frequencies, the anterior pinna flange being largely responsible for high frequency sensitivity in the posterolateral sector.

Potential cues for vertical localisation obtain in transfer function and IID spectra in all 3 species.

Interaural time difference functions obtained for the 3 species were larger than predicted, particularly at low frequencies.

I hereby declare that this thesis is my own work except where the contrary is specifically indicated. No other registration for an award of either the CNAA or any University occurred during the period of this research programme.

Advanced studies undertaken with this programme of research included attendance at seminars and conferences.

June 1988.

D.M.Gower.

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FIGURE PAGE NUMBERS.

Fig.1.1. p25;

Fig.2.1. p46; Fig.2.2. p50; Fig.2.3. p59;

Fig.3.1. p68; Fig.3.2. p71,72; Figs.3.3,3.4. p76;

Fig.3.5. p78,79; Fig.3.6(a,b,c). p82; Fig.3.6(d,e,f). p84;

Fig.3.6(g,h,i). p86; Fig.3.6(j,k). p88; Fig.3.6(l,m). p90;

Fig.3.7. p93; Fig.3.8(a,b,c). p96; Fig.3.8(d). p99;

Fig.3.9. p102; Fig.3.10. p104; Fig.3.11. p106;

Figs.3.12,3.13. p110; Fig.3.14. p112; Fig.3.15. p114;

Figs.3.16,3.17. p117; Fig.3.18. p120; Fig.3.19. p122;

Fig.320. p124; Fig.3.21. p126; Fig.3.22. p129;

Fig.3.23. p132; Fig.3.24. p134; Fig.3.25. p137;

Fig.3.26. p139; Fig.3.27,3.28. p141;

Figs.3.29,3.30,3.31. p144;

Fig.4.1. p148; Fig.4.2. p151; Figs.4.3,4.4. p154;

Figs.4.5,4.6. p158; Figs.4.7,4.8. p162;

Figs.4.9,4.10. p166; Fig.4.11. p170; Fig.4.12. p174;

Fig.4.13. p176; Fig.4.14. p178,179; Fig.4.15. p183;

Fig.5.1. p187; Fig.5.2. p190; Fig.5.3. p192;

Fig.5.4. p195; Figs.5.5,5.6. p197; Figs.5.7,5.8. p200;

Fig.5.9. p203; Fig.5.10. p205; Figs.5.11,5.12. p208;

Figs.5.13,5.14. p211; Figs.5.15,5.16. p214;

Fig.5.17. p216; Fig.5.18. p219; Fig.5.19. p222;

Fig.6.1. p226; Fig.6.2. p229; Fig.6.3. p231;

Figs.6.4,6.5. p234; Fig.6.6. p236; Figs.6.7,6.8. p239;

Fig.6.9. p242; Fig.6.10. p244; Figs.6.11,6.12. p247;

Figs.6.13,6.14. p250; Fig.6.15. p252;

Figs.6.16,6.17. p254; Fig.6.18. p257; Fig.6.19. p259;

FIGURE PAGE NUMBERS (contd).

Fig.6.20, p261; Fig.6.21, p264,265; Figs.6.22,6.23, p269;

Figs.7.1,7.2, p273; Figs.7.3,7.4, p276;

Figs.7.5,7.6, p280;

Fig.8.1, p284.

CONTENTS

Abstract

Declaration

Acknowledgements

Figure Page Numbers

Chapter 1. Introduction.

1.1. Aims ..... p1.

1.2. Psychophysical and behavioural studies ..... p2.

1.2.1. Human studies ..... p2.

1.2.2. Non-human mammals ..... p16.

1.3. Biophysical and Physiological Studies ..... p21.

1.3.1. The human external ear ..... p21.

1.3.2. The guinea pig ..... p27.

1.3.3. The cat ..... p29.

1.3.4. The domestic dog ..... p32.

1.3.5. The Tammar wallaby, *M.eugenii* ..... p33.

1.3.6. The rabbit ..... p34.

1.3.7. Gleaning bats, *M.gigas* and *M.gouldi*..... p35.

1.3.8. IID functions p38

1.4. The Tympanic Membrane ..... p38.

1.5. Concluding Remarks ..... p41.

Chapter 2. Materials and Methods.

2.1. Introduction ..... p44.

2.2. The Anechoic Room ..... p47.

2.3. Sound Production ..... p48.

2.4. Animal Preparation ..... p51.

2.5. Recording and Analysis ..... p56.

2.6. Experimental Modifications of the External Ear p63

2.7. Endocasts ..... p63.

2.8. Modelling ..... p64.

2.9. Concluding Remarks ..... p64.

Chapter 3. Results: The Rabbit.

3.1. Behavioural Observations ..... p66.

3.2. Directional Characteristics of the External Ear ..... p69.

3.3. Head Related Transfer Functions (HRTF's) .... p80.

3.4. Cochlear Microphonic Recordings ..... p115.

3.5. Interaural Intensity Differences ..... p127.

Chapter 4. Results: Further Experiments on the Rabbit.

4.1. Introduction ..... p146.

4.2. Anatomy of the External Ear ..... p146.

4.3. Pinna Removal ..... p149.

4.4. Blocking the Meatus ..... p156.

4.5. Alteration of the Acoustic Impedance of the TM ..... p160.

4.6. Changing the Length of the Meatus ..... p163.

4.7. Experiments on the Tragal Notch ..... p167.

4.8. The Fossa and Anterior Pinna Fold ..... p168.

4.9. The HRTF Nulls ..... p171.

4.10. A Simple Model ..... p180.

Chapter 5. Results: The Rat.

5.1. Anatomy of the External Ear ..... p185.

5.2. Directional Characteristics of the External Ear ..... p188.

5.3. Head Related Transfer Functions ..... p193.

5.4. Cochlear Microphonic Recordings ..... p198.

5.5. Interaural Intensity Differences ..... p206.

5.6. Pinna Flange Removal ..... p212.

5.7. Pinna Removal ..... p217.

5.8. Other Experiments ..... p220.

Chapter 6. Results: The Guinea Pig.

6.1. Anatomy of the External Ear ..... p224.

6.2. Directional Characteristics of the External Ear ..... p227.

6.3. Head Related Transfer Functions ..... p227.

6.4. Cochlear Microphonic Recordings ..... p237.

6.5. Interaural Intensity Differences ..... p245.

6.6. Blocking the Fossa ..... p255.

6.7. Removal of the Anterior Pinna Flange ..... p255.

6.8. Removal of the Pinna Flange ..... p262.

6.9. Removal of the Pinna ..... p266.

6.10. Puncturing the Tympanic Membrane ..... p267.

Chapter 7. Results: Interaural Time Differences.

7.1. Introduction ..... p270.

7.2. The Rabbit ..... p270.

7.3. The Rat ..... p274.

7.4. The Guinea Pig ..... p277.

7.5. Interspecies Comparisons ..... p278.

Chapter 8. Discussion.

8.1. Head Related Transfer Functions ..... p282.

8.2. Azimuthal Directional Characteristics ..... p291.

8.3. Elevational Directional Characteristics .... p295.

CHAPTER 1. INTRODUCTION.

1.1. Aims.

Understanding the mechanisms for assessing sound direction by mammals is proving to be a long and difficult task. A great deal is known about the psychophysics of directional hearing in humans, but relatively little about the behavioural capabilities of other species. Information on the biophysics of the external ear, particularly again in humans, is extensive but comprehensive explanations of tympanic membrane and middle ear function still elude us. Finally, much information has been amassed on neurophysiological aspects relating to directional hearing, but most of this is on species such as the cat and guinea pig.

This thesis investigates the structure and biophysics of the external ear of the European rabbit, Oryctolagus cuniculus (L.), and two rodents, the guinea pig, Cavia porcellus (L.) and the rat, Rattus norvegicus (Berkenhout), in an attempt to identify basic design features. Pinpointing design features may in turn help to shed light on the cues that are employed in directional hearing. It is, of course, not possible to do this without reference to behavioural studies and it is therefore proposed to review both the biophysical and behavioural literature. Furthermore, since there appears to be little fundamental difference between the auditory systems of humans and the other mammals, research findings on humans are also reviewed.

1.2. Psychophysical and behavioural studies.

The behavioural capabilities of the organism must be assessed before any explanations of underlying mechanisms can be attempted.

Unfortunately we know very little about the localisation abilities of most mammals. An important exception is the human but it should be remembered that we are atypical, with large heads and relatively small ears set well down on the sides of the head.

1.2.1. Human studies

The psychophysical literature on directional hearing is extensive and tends to subdivide into studies on time-based and intensity-based cues. ("Intensity" is mistakenly used to mean "sound pressure level" in this field). General reviews are to be found in Mills (1972), Gatehouse (1982), and Lewis (1983). Reviews concentrating on time-based cues are provided by Hafter (1984) and De Boer and Dreschler (1987).

The duplex theory of sound localisation in its basic form is attributed to Lord Rayleigh (1907), who reconciled his earlier position regarding the primacy of intensity cues by conceding that phase difference cues are used at lower frequencies.

The importance of interaural intensity cues had long been realised, (e.g. Rayleigh 1876) but, perhaps because of Helmholtz's apparently expressed belief that the auditory

system is phase deaf, time based cues were not generally accepted as being of importance until Rayleigh's statements of 1907. Indeed, such was Helmholtz's influence in the field that, according to Yin and Kuwada (1984), findings that contradicted his beliefs may well have been suppressed. Certainly, it is now admitted that workers such as Thompson (1877,1878) had discovered the phenomenon of binaural beats and phase based "in-head lateralisation" long before Rayleigh's pronouncements on the matter (see e.g. Hafter (1984)).

Confirmatory evidence for the duplex theory is extensive. Most of the early studies were "in-head lateralisation" experiments using dichotic stimulation; the degree of sidedness of the acoustic image was shown to depend on the extent of the binaural phase or intensity disparity, (see Trimble (1928) for review). Sensitivity to binaural differences was assessed using the just noticeable difference (JND) measure. Thus Schmidt (1955), in a pure tone study, reported that subjects were sensitive to interaural temporal differences (ITD's) as low as 10usec in the lower frequency range but, above 1300Hz, sensitivity dropped sharply. Conversely, sensitivity to interaural intensity differences (IID's) dropped gradually fom a JND of 0.2dB between 2000Hz-5000Hz to 0.8dB at 250Hz. Sandel, Teas, Feddersen and Jeffress (1955) obtained similar findings.

Klumpp and Eady (1956), reported similar JND's using filtered noise; a JND of 9usecs between 150Hz-1700Hz rising

to 62usec for the 3056Hz-3344Hz bandwidth. These authors also reported on pure tone JND's: the average threshold to tones was lowest at 1000Hz (11usec) and at and above 1500Hz the threshold became too high to measure. A similar finding was reported by Zwislocki and Feldman (1956), who showed that interaural phase differences became difficult to detect at and above 1300Hz.

The duplex theory has not gone unchallenged, for example, Stewart (1918), argued that "intensity cannot be an important factor in the location of pure tones." Von Hornbostel and Wertheimer (1920) and also Shaxby and Gage (1932) went even further and argued that localisation could be completely accounted for in terms of time of arrival differences. Conversely, Klemm (1919), in an early time/intensity trading experiment, suggested that time might be reduced to intensity, or to phase and then to intensity on the principle of interference by bone conduction.

Support for the duplex theory has, however, also come from "free field" experiments: for example, Stevens and Newman (1936), testing subjects on the roof of the university building at Harvard, found that the average error of localising tone pulses showed a marked increase in the 3.0kHz region. Mills (1958) produced strong support for the duplex theory using what he called the "minimum audible angle" (m.a.a.) as a measure of directional acuity. Mills defined the m.a.a. as the angle formed at the centre of the head by lines projecting to two (identical) sources of

sound whose positions are just noticeably different when they are sounded in succession. Mills found considerable intersubject variation but the mean m.a.a.'s were as follows: from 250Hz-1000Hz mean m.a.a.'s were between 1° and 2° (when to the front of the subject), from 1000-3000Hz m.a.a.'s rose to 3° dropping back to around 1° at higher frequencies except for a region of reduced acuity around 8kHz. Acuity in the frontal sector was considerably better than at lateral angles where m.a.a.'s of 10° or more were found. These findings have been confirmed by more recent work (e.g. Terhune (1985)) but there is some evidence to suggest that practice substantially improves performance. Mill's subjects appear to have been practised.

Time/intensity trading experiments, where dichotically presented time cues can be used to offset dichotic intensity cues, also show greater subject sensitivity to ITD's at low frequencies and IID's at high frequencies: in other words the trading ratio is frequency sensitive (Feddersen, Sandel,Teas and Jeffress (1957), Whitworth and Jeffress (1961)). Hafter (1984) provides a recent discussion of the literature in this field.

The duplex theory is thus supported by evidence from lateralisation, discrimination and trading experiments and free field experiments of several kinds. It should, however, be noted that the duplex theory as originally stated, refers to the localisation of pure tones: time cues other than phase differences are absent. When brief acoustic impulses are used interaural delays become

useable as lateralisation cues at higher frequencies (see Boring (1942) for a review of early work). The feature given precedence during the localisation of transients is the initial wavefront. Indeed, the bias is so great that perceived location apparently almost always depends on the information received in the first few milliseconds of a complex sound (Wallach et al.(1949), Tobias and Schubert (1959), Gaskell (1983)). This phenomenon is known as the Haas precedence effect. Directional information is, however, also available from ongoing high frequency noise. For example, sinusoidal amplitude modulated waveforms appear to be localised on the basis of the phase differences in the envelopes, e.g. Henning (1974). Non-sinusoidal high frequency waveforms can also be lateralised using envelope information (McFadden and Pasanen (1976)); and recently Bernstein and Trahiotis (1985) have shown a similar effect for low frequency complex waveforms. In the latter study, however, envelope ITD's (i.e. amplitude modulations) were shown to be subdominant to fine structure ITD's (i.e. the waveforms contained within the envelope) in determining lateral position of the acoustic image. Yost (1980) and Hafter (1984) provide recent reviews of this field.

The duplex theory was founded on evidence from lateralisation experiments where the sidedness of the intracranial image was at issue. However, under listening conditions in the field, the sound source position can vary in three dimensions about the listener. As Stevens and

Newman (1936) found, large errors (particularly front/rear reversals) can occur under such conditions, even when the sound source is confined to one plane about the head. Large errors can often be explained as "cone of confusion" effects i.e. as a consequence of identical interaural difference values obtaining for different sound source positions. Mills (1958) avoided this problem by using the m.a.a., but pure tone studies not making use of this technique typically have to discount large errors from the results. A number of authors have, in fact, found that accurate localisation of pure tones is well nigh impossible unless head movements are allowed (see e.g. Wallach (1940), Harris (1972), Terhune (1985)).

Modern free field studies, where the sound source is moved in more than one plane about the subject, are rare, but around the turn of the century, a number of studies were published where the sound source was positioned at various predetermined points on a spherical cage in which the subject's head was centred. A good example of a "sound cage" study is provided by Angell and Fite (1901). Their cage was 2ft in radius and suspended from a ceiling gas fitting. They found that the "more nearly the sounds approach pure tones, the more inaccurate the localisation". They also showed that monaural subjects could localise complex sounds almost as well as normal binaural subjects, particularly after some practice. Indeed, monaural subjects made slightly fewer front/rear reversal errors; monaurals made most of their errors when the sound source was

contralateral to the unoccluded ear. Monaural subjects also made more left/right confusions than binaural subjects, who rarely make this kind of error.

Angell and Fite concluded that "sounds which are complex in nature undoubtedly undergo modification through the damping and reinforcing of their partial tones by the pinna, the external meatus and the head, in a manner which must vary somewhat regularly with variations in the spatial position of the object from which the sound emanates". This remarkable statement is a variation on the Klang or timbre theory of sound localisation (Mach (1875), Bloch (1893)) and is extensively substantiated by recent findings.

Effective monaural localisation of broad band sound has since been reported by Ferree and Collins (1911), Jonkees and van der Veer (1958) and Bauer, Matuza, Blockmer and Glucksberg (1966), and the role of the pinna in localisation has been established by Fisher and Freedman (1968). The latter inserted tubes into the ear canals of their subjects so that pinna effects on the sound field were negated; localisation was clearly disrupted provided no head movements were allowed. Artificial pinnae, attached to the ends of the tubes, restored localisation scores to normal levels.

An intriguing and subsequently influential explanation of how the external ear provides localisation cues has been put forward by the mechanical engineer, D.W.Batteau (e.g.1967). He argued that, when sounds such as clicks are used, the various folds of the pinna bring about a series

of direction specific delays in the incoming sound which are decoded by the C.N.S., perhaps by means of an inverse Fourier transformation. Work with a model pinna revealed distinct elevational and azimuthal delay series, and devices which simulated these effects apparently affected perceived location of the sound source. However, timbre effects were not controlled for and more convincing explanations of monaural localisation as a consequence of such effects have now been put forward (see below). It is also doubtful whether normal external ears produce reflections in the frequency ranges now known to be important in localisation.

The pinna effects a transformation of sound in the frequency/intensity domain, and it is becoming clear that it is the directional dependence of this transformation that is used for localisation. Blauert (1969) reported a free field study where he negated interaural cues using matched loudspeakers placed in the midline at front and back of the subject's head. Third octave bands, of centre frequencies (CF's) between 125Hz and 16kHz, were played alternately from front and rear. Subject assessment of sound source position depended not on which speaker was used but on the frequency band of the sound; from 125Hz to 500Hz and 2000Hz to 6300Hz and also at 16kHz, the source was judged to be at the front; from 500Hz to 2000Hz and 8kHz to 12.5kHz to be at the rear; and at 8kHz to be overhead. In a second experiment, Blauert recorded broadband free field : meatus transformations from his

subjects with the sound played from the front, the rear, and also from above. The ratio of the front to the rear spectrum revealed a difference spectrum boosted between 125Hz to 500Hz and 2000Hz to 6300Hz and at 16kHz. Conversely, this ratio spectrum was depressed between 800Hz to 1600Hz and 8kHz to 10kHz. The match between behavioural and physical data appears to be good. In a third experiment, Blauert stimulated his subjects with broad band spectra, which had been previously shaped using the subjects' own pinnae as filters. The shaping had been done with the sound source either at the front or the rear of the head. All 10 subjects assessed the front recorded spectrum to be coming from the front and the rear recorded spectrum to be coming from the rear, when the sound was played simultaneously from front and rear. Blauert has thus shown that it is cues in the frequency/intensity domain i.e. timbre cues, that influence localisation judgements in the median plane; that these cues are generated by the pinnae; and that in all likelihood, it is the power ratio between clear-cut frequency bands that serve as the cues. Watkins (1978) comes to a similar conclusion from experiments where sound spectra were synthesised using a 2-delay and add system.

Belendiuk and Butler (1975) showed that monaural localisation in the front quadrant of the azimuthal plane was effective only when the upper cut-off frequency of the noise was advanced to 5.0kHz or more. Furthermore, the higher the low pass cut-off frequency, the more accurate

the localisation became. Butler and Flannery (1980) have shown that monaural subjects' judgement of azimuthal location of sound sources correlates closely with the frequency of the signal. With the loudspeaker position kept constant at 90° azimuth (i.e. ipsilateral to the unoccluded ear) assessments of sound source position were requested for noise bands of 1kHz bandwidth with CF's ranging from 4.0kHz to 14.0kHz. As CF's ranged from low to high frequencies, the apparent sound source location moved from 30° azimuth progressively back to 170° azimuth. At 9.5kHz or above (depending on the subject) the apparent location of the sound source switched abruptly to the front again. With further increase in frequency, the sound source was again judged to move gradually rearward. In some subjects there was a third switch to the front at yet higher frequencies (around 13kHz). Monaural subjects thus appear to have two or three "maps of spatial referents" (SRM's) which appear to depend on the frequency perceived. It should, however, be noted that a 1kHz bandwidth centred at 4kHz is a proportionally greater spread of energy (25%) than a 1kHz band centred at 14kHz (7%). Butler and Flannery also report that localisation performance was clearly linked to the number of SRM's spanned by the stimulus; the more SRM's spanned by the noise band, the better. Musicant and Butler (1985) found that binaural judgements show similar distributions with stimulus frequency, at least when the sound source is kept at 90° azimuth. However, when the sound source was moved to 45° azimuth or less, binaural

judgements were clearly the more accurate. The authors concluded that binaural cues dominate judgement when the sound source is between 0° and 45° azimuth but that monaural cues gain ascendency when the sound source is lateral (45°-135°). This agrees with the fact that interaural difference cues change more slowly and less reliably in the lateral sector (see below). Butler (1986) also reported that under broad-band stimulation, binaural localisation was slightly better than monaural localisation, even in the lateral sector. He attributed this to the availability of ongoing interaural phase differences in the binaural condition.

Butler (1987) recorded head related transfer functions (HRTF's) from subjects who had also provided SRM data. There was a good match between individual HRTF's and SRM's; the angle of azimuth at which a particular frequency peaked in the HRTF was the perceived location when bands of that centre frequency were broadcast.

Vertical localisation may also depend on timbre cues. Roffler and Butler (1968) found that subjects' ability to detect sound source position in the frontal region of the median plane improved abruptly when frequencies between 7000Hz and 8000Hz were included in the signal. Roffler and Butler also showed that unobstructed pinnae were necessary for this vertical localisation task. Gardner and Gardner (1973) found that progressive occlusion of the various cavities of the pinna progressively reduced median plane localisation ability. They also reported better performance

for frequency bands at and above 8000Hz and better performance for anterior as opposed to posterior sectors of the median plane.

Bloom (1977) reported that he was able to vary the apparent elevational position of a sound source by altering the frequency at which a notch (a sharp minimum) in the broadcast sound spectrum occurred. For notch positions between 6kHz and 14kHz, the apparent position of the source changed progressively from -45° to +45° elevation. Butler and Belendiuk (1977) showed that recordings made from the ear canals of their subjects, when one of a vertical row of 5 matched loudspeakers was activated, were sufficiently distinct that the subjects could discern which loudspeaker had been used for which recording when the recordings were played back over headphones. Subjects could use not only their own recordings but also other subjects' recordings for this task. Butler and Belendiuk agree with Bloom (1977) in believing that the up-frequency movement of a notch in the HRTF between 6.0kHz and 8.0kHz was the most likely spectral feature being used. Indeed, spectra from the ears of poor localisers showed a less systematic progression of the notch with elevation than did the spectra from the ears of good localisers. Further support for these suggestions comes from a study by Bloom (1977a) where minimum audible field (MAF) measurements were made for monaural subjects. A special point source was positioned at one of 7 angles of elevation in the lateral vertical plane, and MAF's (a measure of auditory threshold) obtained for each position

using narrow band noise with CF's ranging from 4.0kHz to 16.0kHz. Increased thresholds occurred at precisely the frequencies at which individual HRTF notches occurred. The threshold increases also moved up-frequency with increasing source elevation in a similar manner to the HRTF notch. The HRTF notch does therefore appear to be detected.

Individual HRTF's have also been used by Morimoto and Ando (1982) to manipulate apparent sound source locale in both azimuthal and vertical planes, but which spectral features were being used is not clear from this study. Psychophysical studies also have yet to show which parts of the pinna are responsible for generating which sets of cues. Gardner and Gardner (1973) found that occluding the scapha, then the fossa and then the concha, progressively eliminated localisation ability in the median plane. However, like much of the work in this field, the sound source was moved in one plane only, which may have allowed subjects to learn about cues special to this situation.

Searle (1973) and Searle, Braida, Cuddy and Davis (1975) have suggested that additional localisation cues may be available as a result of binaural pinna disparities. HRTF's for left and right ears tend to show differences, particularly in the frequency position of the sharp minimum around 8kHz. Searle et al. (1975) recorded HRTF's for sound sources at various elevations from both left and right ears of their subjects. Playback of the recordings over headphones revealed a greater error rate for the diotic (e.g. left ear recording played to both left and right

ears) as compared to the normal binaural condition. This work has been criticised by Hebrank (1976) because normal binaural cues may have been available owing to imperfect alignment of the subjects' heads in the median plane.

Hebrank and Wright (1974) report that monaural subjects achieved normal levels of proficiency in median plane localisation after a series of training sessions. Subsequent testing with unfamiliar noise resulted in similar increases in error rates for both monaural and binaural subjects. Despite this apparently decisive finding, Searle, Braida, Davis and Colburn (1976) applied a mathematical model, developed from statistical decision theory, to a wide range of publications on localisation in the median plane and concluded that interaural pinna cues are stronger than monaural pinna or shoulder bounce cues. Hebrank and Wright alone have shown that median plane binaural performance can be matched by monaural performance; their approach was unique and until a convincing alternative explanation of their findings is put forward the case for pinna disparity cues is unresolved.

Ivarsson, De Ribaupierre and De Ribaupierre (1980) reported superior binaural performance for median plane localisation, but their subjects were unrestrained and unpractised. Male subjects obtained higher scores for monaural left than for monaural right ear vertical localisation. Ivarsson et al. suggest that this indicates right cerebral hemisphere advantage for localisation tasks (at least in males). This suggestion is supported by the

finding of Altman, Balanov and Deglin (1979) that patients treated with unilateral ECT showed disruption of directional hearing only when the right cerebral hemisphere was shocked. These findings may also explain why binaural median plane judgements tend to be more accurate in studies such as Searle et al. (1975): the binau ral condition ensures that the dominant ear is in use.

1.2.2. Non-human mammals

Low frequency hearing limits amongst the mammals tend to vary directly with high frequency limits to hearing. Each octave change at the high frequency end of the range is associated with more than a 3 octave change at the low frequency end (Heffner and Masterton (1980)). One exception to this rule is the human who would be expected to have a lower limit around 4Hz (at 70dB SPL), instead of several octaves higher at 30Hz. This compression of the hearing range may be linked with the enhanced frequency resolution of humans (Stebbins (1980)).

Heffner and Heffner (1980), Masterton, Heffner and Ravizza (1969) and Heffner and Masterton (1980) argue that in mammals the larger the head, the lower the upper frequency limit. This, in turn, is linked with greater use of ITD cues by the larger-headed mammals. Conversely, smaller mammals have extended high frequency ranges and make more use of IID cues.

Audiograms have been obtained for a variety of mammals. For example:

a) The rabbit, Oryctolagus cuniculus: range, 96Hz-49kHz at 60dB SPL with threshold minima at 2kHz and 16kHz (Heffner and Masterton (1980)). For Chinchilla strain rabbits Borg and Enstrom (1983) report threshold minima at between 5kHz and 16kHz.

b) The albino rat, Rattus norvegicus: range, 250Hz-80kHz at 70dB SPL; threshold minima at 8kHz and 38kHz. (Kelly and Masterton (1977).

c) The domestic cat, Felis catus: range, 50Hz-60kHz at 40dB SPL (Miller, Watson and Corell (1963)) with a threshold minimum at 8kHz (Neff and Hind (1955)).

d) The guinea pig, Cavia porcellus, range, 86Hz-46.5kHz at 50dB SPL, with a threshold minimum at 8kHz and indications of a second minimum around 1kHz in some animals (Heffner, Heffner and Masterton (197?)).

Work on the directional acuity of terrestrial mammals has been reviewed by Gourevitch (1980, 1987). Most of the information has been obtained from : a) "approach to target" experiments where the animal is required to move to one of two or more sound sources. The signal is sometimes repeated or even continuous and head and pinna movements may aid localisation: b) minimum audible angle measurements where the animal is trained to press a lever (followed by a reward if correct) when the position of the sound source changes. A variation on the latter technique is the conditioned suppression technique where the animal is trained to lick or drink fom a particular place; a change in the position of the sound source is followed by an

electic shock. If the animal detects the change, expectation of the shock will automatically suppress the consummatory behaviour.

There are indications that the different methods of testing for directional acuity yield slightly different results but no systematic testing of this has yet been carried out.

The highest acuity yet reported is 4° azimuth (at 1kHz) for Macaca mulatta and M. nemestrina, the rhesus and pig-tailed macaques (Brown, Beecher, Moody and Stebbins (1978)). Heffner (1975) reported that mongrel dogs could discriminate click sources about 4° apart and Casseday and Neff (1973) reported angular thresholds of 5° for domestic cats, again using wide band noise. However, performance for pure tones in the latter species was poorer, being 8° or 9° for pure tones between 0.5kHz and 2 kHz (Casseday and Neff (1973)). Jenkins and Merzenich (1984) reported that cats localised single noise bursts or tone pips of 40usecs duration when the sources are 30° apart in the frontal sector. Stimuli of such short duration negate the possible use of head or pinna movements in the localisation task.

Directional acuity in the rat is relatively poor. Kelly and Glazier (1978) found that the mean localisation threshold of the albino rat to click trains was approximately 28°, and Heffner and Heffner (1985) have confirmed this using a conditioned suppression technique in the wild Norway rat.

The Kangaroo rat Dipodomys merriami is slightly better

with a mean localisation threshold of 20° (Heffner and Masterton (1980)).

A number of mammals show a bimodal distribution of localisation errors when tested with pure tones. Thus the rat shows an increase in errors at 8kHz (Masterton, Thompson, Bechtold and RoBards (1975)), the kangaroo rat at 4kHz (Heffner and Masterton (1980)) and the cat at 4kHz (Casseday and Neff (1973). These regions of poor performance are reminiscent of the 3kHz peak in human localisation error scores (e.g. Stevens and Newman (1936)) and indicate that the duplex theory may be applicable to non-human mammals. Lateralisation experiments on primates and cats confirm this. Thus Wegener (1974) reported that rhesus monkeys showed a mean ITD threshold of 53usecs to dichotically-presented tones of 1kHz and a mean IID threshold of 2.7dB. Similar findings are reported for M. nemestrina by Houben and Gourevitch (1979). A better performance is reported by the latter authors for one rhesus monkey which showed an IID threshold to clicks of 2.55dB and an ITD threshold of 27usecs. Wakeford and Robinson (1974) found IID thresholds of 0.5dB (3kHz) and 1.5dB (500Hz) and ITD thresholds of 25usecs (500Hz and 1000Hz) and 80usecs (2kHz) for the cat. These latter findings are much closer to human thresholds (of about 1dB and 11usecs) than the thresholds of other mammalian species and may reflect the fact that the cats were required to detect reversals of the dichotic tone bursts to a lead or gain by the opposite ear.

Almost all the localisation studies on non-human mammals have confined the stimulus source to one horizontal plane. The one exception appears to be Brown (1982) who reported vertical m.a.a.'s of about 10° for two pig tailed macaques when macaque "harsh" calls were used as the signal. Vertical m.a.a.'s for a macaque "clear" call were larger, the best being about 19°. Brown estimated that the acuity of vertical localisation is inferior to that of horizontal localisation by a factor of approximately 2.5. This factor in the human is estimated to be 2.3 (Hausler, Colburn and Marr (1979)). Brown also reported that frequencies above 2kHz had to be present in the signal for the macaques to score well on the vertical localisation task. Reflections from the animals' torsos may have been providing the elevational cues at the lower frequencies. Brown also reported that localisation is more accurate in the frontal azimuthal angles as compared with the lateral angles.

Monaural directional capabilities have been investigated for guinea pigs (Clements and Kelly (1978)), rats (Judge and Kelly (1981)), and gerbils, Meriones unguiculatus (Kelly and Potash (1986)). No indication of monaural localisation ability was found in any of these species. However, the localisation tasks always involved left/right or multiple choice discriminations involving both sides. The use of timbre cues by non-human mammals is not ruled out by these results.

Masterton et al.(1975) tested left/right discrimination in cats, tree shrews, rats and hedgehogs. Whereas cats and

tree shrews performed well at low frequencies, rats performed poorly and hedgehogs failed to make any successful discrimination until tones of 8kHz or above were used. The authors concluded that hedgehogs do not use interaural phase differences for localisation of sound. Indeed, the frequency/intensity domain may be the only domain used by hedgehogs for localisation. This fits in with the observation made by Masterton et al. that whereas the lateral superior olivary nuclei (LSO) are large in the hedgehog, the medial superior olivary nuclei (MSO) appear to be absent. The LSO appear to be associated with the analysis of IID's and the MSO with ITD's in mammals (see below).

1.3. Biophysical and Physiological Studies.

1.3.1. The Human External Ear

Not long after Darwin had proposed that the various folds and prominences within the human pinna were rudiments of the structures used to support the larger ears of lower mammals, (see Butler 1975), Mach (1875) suggested that the pinna acted as a resonator which affected perceived timbre. This suggestion was supported by Bloch (1893) who had found that median plane localisation was impaired when the upper parts of the pinna were filled with wadding and when the lobules were taped to the skull. Lord Rayleigh (e.g. 1907) was also of the opinion that the pinna affected perceived

timbre. He suggested that front versus rear discrimination was made on the basis of "quality" differences caused by the external ears, and that it was the "higher elements of the sound" that changed. However, Rayleigh (1904) had by this time already published his calculations on the "acoustic shadow of a sphere", which neatly explained why substantial IID's occurred at higher frequencies only; the ears needed only to be regarded as simple pressure detectors on the surface of a sphere for interaural differences to be explained. The role of the external ears in directional hearing therefore appears to have been regarded as a minor one and general interest in the external ears was not reawakened until workers such as Batteau (1967) published their findings.

A detailed biophysical examination of the external ear was conducted by Weiner and Ross (1946). They inserted a fine probe into the meatus until the subjects reported scraping or thumping noises. The probe was then withdrawn a set distance from the tympanic membrane (TM). The HRTF at 45° (i.e. on axis to the pinna) peaked to 22dB at 3kHz and maintained a shelf or shoulder of 17dB or more from 4-6kHz. A sharp minimum or null tended to occur around 8KHz. Weiner and Ross argued that diffraction by the head could account for only a small part of the acoustic amplification of the ear, and that most of the gain was caused by ear canal resonance. Weiner (1947) subsequently published measured IID functions for several angles of azimuth which showed that IID's depended principally on ipsilateral gain (and

not contralateral loss caused by "head shadow"). Yamaguchi and Sushi (1956) subsequently showed that HRTF gain in the 4kHz-5kHz region originated as concha, and not meatus, standing wave resonance.

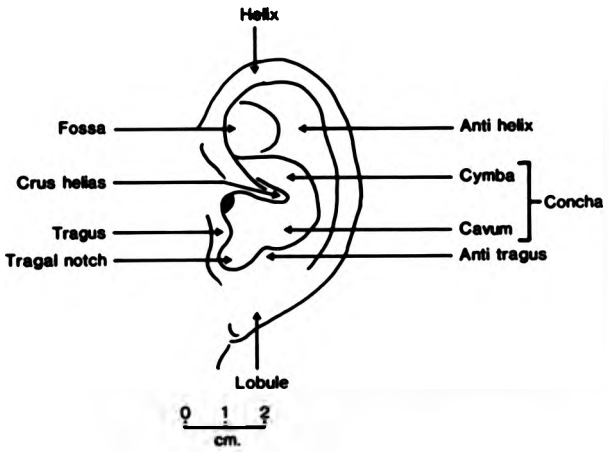
Shaw (1974, 1982, 1982a), in reviews of his work since 1966, also explains much of the behaviour of the external ear at higher frequencies. The primary ear canal (quarter wavelength) resonance is at 2.6kHz (21dB at 60° azimuth) and beyond this a strong concha resonance sustains the response (around 17dB at 60° azimuth) up to about 6kHz. Although this fundamental depth resonance (quarter wavelength) is strongly coupled to the sound field, diffraction by the pinna extension results in substantial and progressive losses in gain (10dB or more) in the 4kHz-6kHz region as the sound source is moved rearward. These losses are clear indicators of the angle of azimuth from which a particular HRTF is obtained. A sharp minimum occurs around 9.5kHz followed by a covert maximum at about 12kHz. The precise frequencies at which these features occur depend primarily on the elevational position of the sound source. The greater the elevation of the source, the higher the frequencies at which the features occur.

In order to minimise "contamination" by diffraction and reflection from the head, Shaw used a nearby point source at grazing incidence to investigate the behaviour of the pinna at higher frequencies. The meatus was blocked and the probe positioned at the centre of the meatal plug.

Six modes were identified: 1) 4.3kHz, the fundamental

Figure 1.1: Drawing of a human pinna (left).

Fig. 1.1


Helix
Fossa
Anti helix
Crus helias
Cymba
Concha
Tragus
Cavum
Tragal notch
Anti tragus
Lobule
0 1 2
cm.

depth resonance of the concha; 2) 7.1kHz, and 3) 9.6kHz, both transverse and maximally excited from +75° elevation; these latter two modes collapsed into a single mode at about 9kHz in models where the fossa was filled (a drawing of a human external ear is shown in Fig.1). Modelling experiments also revealed that a horizontal barrier (the crus helias) had to be present in order to divert airflow towards the rear of the concha and thereby increase its effective length; 4) 12.1kHz, 5) 14.4kHz, and 6) 16.7kHz are all transverse modes maximally excited from the front. Mode 4 is clearly linked to the breadth of the concha because varying this in modelling experiments resulted in concomitant frequency changes in the mode.

Shaw found that HRTF's varied considerably in their details. For example, in some individuals the elevation dependent up-frequency march of the features in the 7kHz-12kHz range did not occur; there were also considerable differences between the left and right ears in some subjects.

Mehrgardt and Mellert (1977) have confirmed some of Shaw's results; e.g. the elevation dependency of HRTF features in the 7kHz-12kHz range.

The biophysical findings on the external ear help to explain some of the psychacoustical findings: Butler's SRM 1 equates with concha modes 1 and 2 and SRM 3 roughly equates to modes 4, 5 and 6. SRM 2 however appears to equate to mode 3, which is more sensitive to elevational than to azimuthal changes in source position. Modes 3 and 4

occur on either side of the notch shown by Bloom (1977, 1977a) and Butler and Belendiuk (1977) to be important in elevational judgements.

Roles for the helix and tragal notch have yet to be ascertained and the treatment of the ear canal as a uniform tube terminated at right angles by the TM is, of course, an oversimplification. Stinson (1985,1987) has shown that above 8kHz the details of ear canal geometry, including its curvature and variation of cross sectional area must be known before the details of the pressure distribution along the canal (and also across the TM) can be fully explained. Khanna and Stinson (1985) come to similar conclusions from their work on the ear canal of the cat.

The role of the head and torso in generating potential localisation cues has been explored by Kuhn (1982). In the azimuthal plane, head "obstacle" effects result in SPL differences between the 2 sides of the head that can exceed whole system IID's. However head generated differences lack the sharp frontal directivity of the HRTF IID's. The torso contributes substantially to median vertical plane directivity. Indeed at 1.0kHz, torso effects are responsible for most of the gain directed at the ear canal: maximum gain occurs around -160° (below, back) and -40° (below, front). There is, however, no evidence, as yet, to show that humans utilise these potential cues.

1.3.2. The Guinea Pig

Sinyor (1971), investigated the guinea pig external ear by means of probes inserted into the base and opening of

the ear canal. Pure tones up to 15kHz fom various angles of azimuth were presented to anaesthetised or moribund animals. The HRTF at 90° azimuth (0° elevation) peaked to 12dB at 2.5kHz, dropped to around 5dB between 3.0kHz and 4.5kHz and showed a series of smaller peaks (up to 8dB) from 5.5kHz to 10kHz. From 10kHz to 15kHz, the function became irregular. Sequential removal of the pinna flange and concha revealed the 2.5kHz peak to be associated with the ear canal. The concha resonance peaked to around 15dB at 6.5kHz but this is offset, to some extent, by losses associated with the ear canal in this frequency region. The pinna flange was also responsible for "on-axis" gain at a number of frequencies and most of the directionality shown by the HRTF's appears to be attributable to the pinna flange.

The mean length of the guinea pig ear canal is estimated by Sinyor to be 0.87cms. The quarter wavelength resonance might therefore be expected to be around 10kHz. Instead resonance was established in the canal at 2.5kHz. Experiments where the bulla was filled with water, or where diseased middle ear specimens were investigated, revealed that, when the acoustic impedance of the TM was increased, resonance did indeed occur at higher frequencies. The apparent cause of the low frequency resonance in the normal guinea pig ear canal is the close match between the acoustic impedances of a narrow ear canal and a TM of relatively low impedance.

Sinyor also reports that there was little difference

between the HRTF's of anaesthetised and freshly sacrificed guinea pigs.

1.3.3. The Cat

HRTF's for the cat were reported by Weiner, Pfeiffer and Backus (1966) who implanted a fine probe into the base of the ear canal. The "on-axis" HRTF showed a strong peak of 20dB at 4kHz dropping to -3dB at 13kHz. A second probe positioned near the tragus enabled ear canal gain to be calculated. This peaked at 4kHz or higher, depending on the individual, and is presumably the quarter wavelength resonance of the canal. The broadness of the peak is explained by the complex shape and distal broadening of the canal. (The ear canal is 2cm long in all, the distal 0.5cm broadening to about twice the initial cross-sectional area). Removal of the pinna in two cats enabled the "on-axis" gain curve to be calculated. This showed an initial peak of 10dB at about 2.5kHz, a dip at 3.5kHz and a subsequent broad maximum of approximately 7dB around 5kHz. The HRTF is thus a composite of pinna and ear canal gain, with the latter filling in the dip in the 3.5kHz-4kHz region. The threshold minimum in the cat audiogram is actually at 8kHz (Neff and Hind 1955). Moller (1965) suggests that this may be accounted for by the fact that the cat middle ear is divided into two volumes connected by a small hole. In an investigation of cat single auditory nerve fibres, Kiang, Watanabe, Thomas and Clark (1965)

found a clear elevation of threshold around 4kHz.

Weiner et al. (1966) found that the cat HRTF's became strongly directional in the azimuthal plane from about 3kHz onwards. Elevating the sound source to +45° resulted in a gain of about 7dB in the 8kHz region.

IID functions for both adults and kittens have been obtained by Moore and Irvine (1979). Large IID's of 20dB or more occurred from about 5kHz onwards in adults and older kittens, but did not occur until 10kHz or more in the younger kittens. These findings have been extended by Irvine (1987) who also reported marked variations in contralateral ear SPL's around 6kHz-8kHz, which he explained in terms of interference between sets of creeping waves propagated around the head in each direction.

A more detailed study of the directionality of the cat ear has been reported by Phillips, Calford, Pettigrew, Aitkin and Semple (1982). They monitored the amplitude of the cochlear microphonic (CM) when sound was presented in both vertical and horizontal planes in the frontal hemifield. The data were presented in the form of isointensity contours, thus avoiding inherent calibration problems. Phillips et al. found that the directionality of the ear increased with increasing frequency and that pulling the recorded pinna medially resulted in corresponding changes in the CM isointensity contour plots. Removal of the recorded pinna resulted in both loss of CM "on axis" amplitude and loss of directionality. The reported reduction of as much as 25-30dB at 3.5kHz as a consequence of pinna removal is

remarkably high and may be accounted for (as Coles and Guppy (1986), point out) by the fact that some of the ear canal was also removed during this procedure. Flynn and Elliott (1965) monitored behavioural audiothresholds in cats before and after pinna removal and the maximum loss was found to be no more than 20dB.

Phillips et al. also reported changes in pinna axis with frequency. However, the pinnae may not have been held in the normal "alert" position in these experiments so this finding should be treated with caution.

Calford and Pettigrew (1984), using similar techniques to those of Phillips et al. (1982), explained the directionality of the cat's pinna in terms of diffraction at a circular aperture. The best fit between the solid angle subtended by the 5dB isoattenuation contour and calculated theoretical curves was for an aperture of 6cms diameter. This approximates more closely to the length of the long vertical diameter rather than the mean diameter of the pinna opening. Calford and Pettigrew also report that pinna axis shifts with frequency may be sensitive to the details of pinna posture. Cutting the skin and muscles on the dorsal surface of the skull to facilitate head holder attachment causes the pinnae to drop into unnatural positions. Calford and Pettigrew stated that they had the impression that more natural pinna postures might result in greater uniformity of the pinna acoustic axes at the various frequencies.

The cat has also been used to study the physical basis of

potential time based cues. Thus Roth, Kochlar and Hind (1980) obtained ITD functions for 6 angles of azimuth. ITD values for particular angles of azimuth showed gradual decreases with increasing frequency. Retraction of the pinnae resulted in slightly smaller ITD values and a slight decrease in the "roughness" of the ITD functions. However, most of the roughness was shown to be caused by the table on which the animals were supported. Measurement of ITD's is typically done on the steady state form (ITDp). Within certain frequency limits, phase velocity tends to decrease with increasing frequency because the wave front near the surface of an object is a combination of incident and scattered waves and the scattered pressure distribution is a function of wavelength. A medium in which the phase velocity shows frequency dependence is a dispersive medium and Roth et al. argue that, for complex signals in dispersive media, the signal energy is transported as a "group" or "packet". The "group" ITD based on "group velocity" is also available as a cue. Group ITD's are likely to differ significantly from steady state ITD's, in the frequency range where phase velocity is frequency sensitive.

1.3.4. The Domestic Dog.

Gorlinskii and Babushina (1985) have recently investigated the directionality of the external ear of what they chose to call "randomly bred" dogs. They found a gradual increase in directionality with increasing

frequency and a change in acoustic axis when the recorded pinna was rotated. No HRTF's were reported and measurements were confined to the azimuthal plane.

1.3.5. The Tammar Wallaby, Macropus eugenii

Hill and Coles (1981) and subsequently, Coles and Guppy (1986), have given a detailed account of the biophysics of the external ear of the Tammar wallaby. A probe microphone was implanted into the proximal end of the ear canal wall of fresh cadaver heads. The "on axis" HRTF typically peaked to around 27dB at 5kHz dropping to around 0dB around 30kHz. Removal of the pinna resulted in a function which peaked to 15dB between 5kHz and 8kHz, dropping to 0dB at 10kHz. The ear canal is reported to be about 1.6cm in length. The quarter wavelength resonance would be expected at about 5.5kHz and this appears to fit with the observed results. Coles and Guppy argue that the pinna itself behaves like a conical horn: the pinna gain curve (the ratio of the normal HRTF : pinna-removed function) is similar to the calculated gain function for a finite-length conical horn of similar dimensions. Also, enlargement of the pinna did not result in any noticeable down-frequency shift in HRTF features; something to be expected if pinna induced standing wave resonances were contributing to the HRTF. The Tammar wallaby external ear thus appears to be distinctly different from that of the human and guinea pig, both of the latter showing concha associated resonances.

Coles and Guppy also reported on the directionality of

the Tammar wallaby ear, displaying their results in the form of isointensity plots at selected frequencies. Directionality increased sharply above 4kHz and thereafter increased steadily with frequency. This systematic decrease in the acceptance angle with increasing frequency was shown to equate to the directivity pattern for sound diffraction at a circular aperture. Despite the oval shape of the pinna opening, the agreement between predicted and measured directionality was good. However, elevation and azimuthal components had to be plotted separately in order to achieve this. The pattern of occurrence of minima or "nulls" (displayed in a series of polar plots) was also explained in terms of diffraction at a circular aperture. Of particular note is the finding that nulls are more prominent near the leading edge of the pinna and that, with increasing frequency, these nulls gradually approach the midline (from the contralateral side). A consequence of this is that IID's will be particularly large in the frontal sector with increasingly sharp rises from 0° azimuth as frequency increases. The acoustic axis of the pinna was also shown to vary with frequency; most notably, low frequencies tended to be "on-axis" around -15° elevation, while higher frequencies (8KHz or more) were "on-axis" at 0° elevation.

1.3.6. The Rabbit.

Fattu (1969) has investigated the directionality of the rabbit ear using a model with a microphone inserted

directly into the base. Large amounts of gain and fluctuating directionality with frequency were reported but these may be overestimations caused by substituting the TM by an object (the microphone) of higher acoustic impedance. Fattu also chose to direct the model ear rearward for this study.

1.3.7. Gleaning Bats. Macroderma gigas and Nyctophilus gouldi.

Guppy and Coles (1988) have reported on the biophysics of two species of gleaning bats using a probe microphone inserted through the auditory bulla so that the microphone occupied the position previously occupied by the TM. (Cadaver heads were used in this study).

In M. gigas the HRTF rose sharply to 30dB or so, peaking between 4.5kHz and 6.5kHz, depending on the individual. Thereafter the HRTF dropped non-monotonically to 0dB between 60kHz and 100kHz. Removal of the pinna resulted in a transformation function that peaked sharply to 17dB at 7.8kHz. This approximates to the predicted quarter wavelength resonance of the ear canal (length 1.1cms). Calculated pinna gain curves peaked to 18dB between 5kHz and 7kHz and, thereafter, fluctuated around 10dB. At the lower frequencies the pinna gain curve resembled the calculated gain curve for a conical horn of the same dimensions but, at higher frequencies, pinna gain dropped below that expected for a conical horn. Guppy and Coles suggest that this may be a consequence of the irregular

shape of the pinna.

The HRTF for the smaller N. gouldi is similar to that of M. gigas but best gain is reduced to 23dB or less and occurs at higher frequencies. Ear canal resonance is not discernible in N. gouldi, perhaps because of the shortness of that structure (0.25cms).

Directionality of both species' external ears increases with frequency and approximates to the diffraction patterns at a circular aperture. The acoustic axes of the pinnae shifted medially and upwards with increasing frequency. These axis shifts are reminiscent of human HRTF feature shifts but the causes may be different. The cone shaped bat pinna is obliquely truncated in both vertical and horizontal planes and Guppy and Coles suggest that it is this asymmetry that causes the axis shifts. Guppy and Coles state that, in an asymmetric horn, wave fronts travelling along the longer side will tend to be delayed relative to the wavefronts travelling along the shorter side. The phase lag between the two sides will result in subtraction of energy from the total acoustic input when it exceeds 180°. The largest useful mouth is therefore likely to occur when the path length from the normal (right-angled) truncation point to the tip of the long side is half the wavelength. Thus longer wavelengths will tend to be maximally amplified when at normal incidence to the mouth of the pinna, but shorter wavelengths, because of increasing phase cancellation effects, will show more net gain as the direction of the wavefront approaches parallelity to the

longer side. Guppy and Coles suggest that the expected position of the acoustic axis (x) can be approximated by:

$$\mathrm{Cot}(x+y) = \frac{2a\ \mathrm{Sin}b}{(w/2)-2a\ \mathrm{Sin}b}$$

where y is the angle of offset of the pinna from the midline (for azimuth effects) or the horizontal 0° plane (for elevational effects), a is the radius of the mouth at the truncation point, w is the wavelength, and b is the angle between the approximate truncation plane and the extended edge of the horn.

Theoretical determination of the acoustic axes for both species of bats agreed quite well with the experimental observations. Guppy and Coles also investigated the effects of tragus removal on the directionality of the pinna. Other than a slight relocation of the acoustic axis and some null positions, there were no noteworthy consequences of this operation. This finding contrasts with that of Lawrence and Simons (1982) who found that deflection of the tragus in Eptesicus fuscus degraded behavioural vertical acuity from 3° to about 12°-14°. Lawrence and Simons reported that the tragus was associated with a strong echo, 45usecs-60usecs after primary impulse arrival. Explanations of localisation based on this kind of cue are, however, difficult to reconcile with frequency/intensity domain explanations which, at present, are dominant in this field.

1.3.8. IID Functions.

Calculated IID functions have been used by some authors to estimate potential auditory acuity. Thus Harrison and Downey (1970) calculated best minimum angles of 1.125° for the squirrel monkey, 2.0° for the bat, Phyllostomus hastatus, 1.5° for the rat, and 1.125° for man. These estimates are based on JND's of 0.5dB for each species. Similarly, Moore and Irvine (1979) calculated a best minimum angle of about 1.2° for the cat. Only in the case of man do these estimates approach actual behavioural localisation proficiency levels. It would appear that other species do not perform to their maximum capabilities in behavioural tests of localisation.

1.4. The Tympanic Membrane

TM action affects the sound transmission properties of both the external and middle ears. Von Bekesy (1941), after point by point measurements with a capacitative probe, reported that the human TM appeared to behave as a stiff plate hinged superiorly around the ossicular axis, a "lower fold" in the TM providing the necessary give for this type of displacement. The middle ear transform would therefore be given by the area ratio between the effective area of the TM and the stapes footplate. Moller (1961) and Zwislocki (1962) developed acoustical networks describing middle ear function based on this notion of TM operation. Such networks worked well up to 2kHz but thereafter failed

to predict the large energy losses at higher frequencies. The development of time-averaged holography techniques (e.g.Khanna and Tonndorf (1972)) provided the answer: at lower frequencies the TM behaves as a simple elastic shell but, at higher frequencies, the TM vibration patterns break up into isolated zones, the manubrium mallei being driven directly by ear canal sound pressure. (This is actually shown more clearly in the cat than in man.) Thus at higher frequencies the TM is decoupled from the middle ear mechanism and serves merely as a baffle for the manubrium (thus preventing pressure difference effects).

Tonndorf and Khanna (1972) have resurrected a proposal first made by Helmholtz (1868) that (at lower frequencies) the TM itself acts as a transformer as a consequence of the curved membrane effect. They suggest that the elasticity of the TM is conferred by sliding effects between the various TM fibres and the matrix or ground substance of the TM, the sliding causing stretching of the bonds between fibres and matrix.

Air pressure differences across the TM are known to reduce cochlear microphonic voltage, regardless of the direction of the difference (Wever and Lawrence (1954)). This is primarily the result of increased TM stiffness but Tonndorf and Khanna argue that a change in TM transformer ratio may also take place under these circumstances. TM perforations also tend to reduce middle ear transmission, but for a different reason, namely loss of the baffle effect (McArdle and Tonndorf (1968)).

An updated acoustical network for the middle ear taking the compound eardrum finding into account is given by Shaw (1982).

In many mammals the TM has two distinct parts, a taut pars tensa and a limp pars flaccida, otherwise known as Shrapnell's membrane. Tonndorf and Khanna (1972) reported that coating the TM, and in particular the pars flaccida, with large quantities of metallic powder resulted in an immobilisation of the manubrium. For free manubrial movement the pars flaccida must be free to move. This is because it is flat and lies relatively far lateral to the ossicular axis and small manubrial movements therefore result in large movements of the pars flaccida.

Stenfors, Saten and Winblad (1979), however, have reported that in rats the pars flaccida appears to act as a safety valve. Middle ear pressure changes are reacted to instantly by lateral displacement or, in extreme cases, by perforation of the pars flaccida. Only when the rat swallowed did the eustachian tube function to equalise pressure on either side of the TM.

Kohlloffel (1984), however, points out that there is considerable variation in the size of the pars flaccida. In some mammals (e.g. pig, goat) the pars flaccida is larger than the pars tensa, whereas it may be absent altogether in other species (e.g. mole, guinea pig, red squirrel). In most species the cavity above the pars flaccida, (the epitympanic cavity) is connected to the tympanic cavity via the isthmus tympanicus. Kohlloffel argues that such an

arrangement allows of an acoustic shunt around the pars tensa which results in transmission loss at low frequencies but transmission gain in a frequency band below pars tensa resonance frequency. The naturally occurring dehiscences of the hare (Lepus europaeus) TM may have the same effect (although the hare TM contains a small pars flaccida). In the goat and sheep, the isthmus tympanicus is narrow and, since mass reactance in the isthmus will rapidly exceed the stiffness reactness of the pars tensa and bullar cavity, intercavity flow will cut off at rather low frequencies (e.g. 450Hz in the goat). In the pig there is no patent isthmus tympanicus and the large pars flaccida and its associated epitympanic cavity are likely to act in front of the TM as a Helmholtz resonator. This will result in loss of gain in the ear canal for a specific frequency band. It may be that such a device renders the ear canal less echoic at these frequencies. Species with large Shrapnell's membranes tend to lack low frequency sensitivity whether or not there is a patent isthmus, however, and it is clear that much work still needs to be done before the role of the TM is fully understood.

1.5. Concluding Remarks.

The termination of the external ear thus undoubtedly affects the way in which that structure is coupled to the sound field. It is not pertinent here to discuss details of transmission beyond the TM, studies of middle and inner ear function being distinct fields in their own right. It is

worthy of note, however, that work on the central auditory system has produced much to support behavioural findings. The generally tonotopic organisation of central auditory tissue and the nature and extent of binaural interactions at the neuronal level are of particular interest. Reviews of work on the mammalian central auditory system are to be found in Erulkar (1972), Syka and Aitkin (1981), Masterton, Glendenning and Nudo (1982), Masterton and Imig (1984) and Phillips and Brugge (1985).

One of the first points at which binaural interactions take place is the principal neurones of the lateral superior olive (LSO) where ipsilateral excitation and contralateral inhibition is the rule. The principal neurones are sharply tuned (mostly to higher frequencies) and are primarily IID sensitive. Conversely, the medial superior olive (MSO) principal neurones tend to be tuned to lower frequencies and are mostly ITD sensitive. About 75% of the latter are EE type (excited by either ear) and it is these neurones that are delay sensitive (Galambos, Schwartzkopf and Rupert, (1959)). Animals with well developed MSO's (e.g. humans, cats, dogs, monkeys, tree shrews and elephants) readily localise low frequencies whereas species with small (the rat), or no MSO's (the hedgehog) have poor low frequency localisation.

The superior olive nuclei thus show a compartmentalisation of function that parallels behavioural findings.

Axons from the superior olive and other hind brain nuclei converge upon the inferior colliculus (IC) of each side.

Unilateral IC destruction severely disrupts localisation in the contralateral hemifield. ITD and IID sensitive neurones are found throughout the central nucleus of the IC but there is little sign of the topotopic organisation shown by the homologous tissue (nucleus mesencephalicus lateralis dorsalis) in the barn owl (Tyto alba). (See Knudsen (1987) for review).

Space preferring neurons have been identified in the deep layers of the mammalian superior colliculus (e.g. Palmer and King (1982)), but these neurons have very slow response rates and seem to be involved in collating auditory space with visual and other sensory information. The auditory cortex of echolocating bats (Suga (1981), Suga and Horikawa (1986)) appears to contain topographic representations of a number of sound stimuli features but there is no evidence of such representation in non-echolocating mammals. At present, the indications are that it is the activity profiles of large populations of neurones that specify sound source locale; and the IC is the likely seat of such profiles. Whether or not separate analysis of monaural and binaural input takes place at the higher levels remains to be determined, but it should be remembered that binaural spectra will be similar to, if not identical with, monaural spectra for low intensity sounds when contralateral ear input drops below threshold.

CHAPTER 2. MATERIALS AND METHODS

2.1. Introduction.

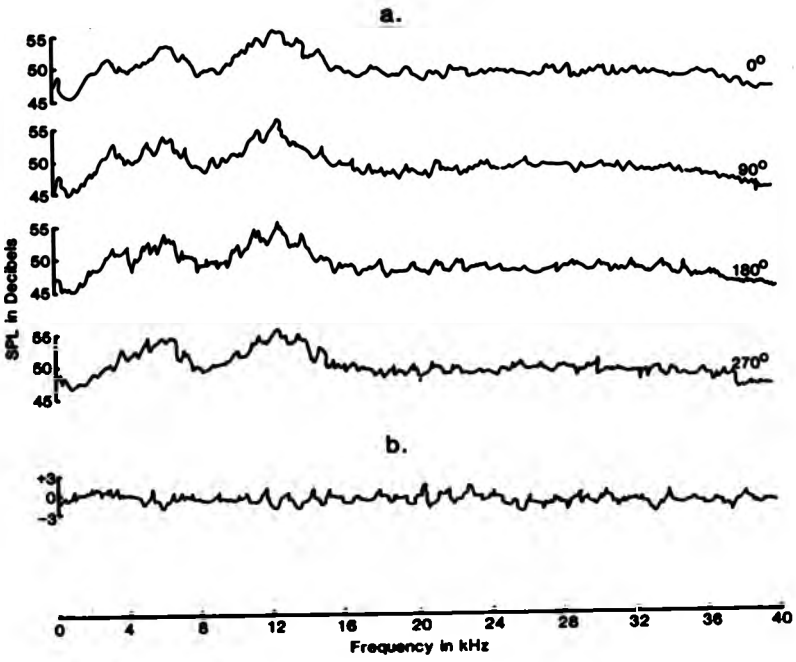
The external ears of anaesthetised or dead mammals have been investigated in terms of their gain functions and directional properties. Implanted probe microphones or cochlear microphonic (CM) potentials were used to monitor pure tone or broad-band sound SPL changes with changes in position of the sound source or to the ear. The details of the technique have, however, changed with time. Since space does not permit of a detailed chronological account of these changes, they will be described in outline to begin with, and actual details of the techniques will be given later.

Initially probe microphones were implanted directly into the base of the ear canal of cadavers (rabbits) and SPL's monitored for every 10° azimuth using pure tones from 500Hz to 32kHz. A Bruel and Kjaer (B & K) frequency analyser was initially used for measurement but, in order to speed up data collection, a B & K level recorder, which allowed of rapid data collection in the form of polar plots was subsequently used. It was also decided at this time to collect data from not just the azimuthal plane but also from other horizontal planes both below and above the level of the head. Changes in phase angle as the sound source was moved around the head were also monitored during the course of some experiments.

Again because of the need to increase speed of data

Figure 2.1: (a) Four sound spectra recorded at the centre of the test chamber. The sound source has been positioned at 90° intervals in a horizontal plane 1m above floor level; (b) Resultant ratio of the spectra recorded at 90° and 270°.
(Sound source was a Technics type DF05 tweeter The spectra are averages of 32 samples and adjusted to account for the microphone correction factor.)

Fig. 2.1


a.
55
50
45
0°
90°
180°
270°
SPL in Decibels
b.
+3
0
-3
0
4
8
12
16
20
24
28
32
36
40
Frequency in kHz

collection, and also because a more detailed frequency analysis was felt to be desirable, the use of high resolution signal analysis using broad-band sound was developed. Because of the acoustic impedance changes that inevitably result from probe microphone implantation it was also felt desirable to monitor directional changes using CM's. This was done first on the guinea pig and high resolution signal analysis was also applied to this data. It rapidly became clear that many of the more interesting directional effects were occurring at frequencies above the range of the signal analyser (20kHz) and so the CM was recorded on an instrumentation recorder and subsequently played back at half speed into the signal analyser giving a frequency range up to 40kHz.

CM's were subsequently monitored in the rabbit and rat, but in the rabbit studies the CM was not monitored above 20kHz.

Towards the end of this study a high performance probe was developed which minimised the consequences of implantation. Much of the detailed bioacoustic analysis was carried out using this in conjunction with the analysis techniques developed previously.

Throughout the study, endocasts of the external ears of the experimental subjects were made whenever possible.

2.2. The "Anechoic" Room.

All data collection was made in an "anechoic" or more

strictly speaking, a hypoechoic chamber of internal dimensions 2.5 x 2.5 x 2.2m lined with rockwool wedges on all internal surfaces. Acoustic conditions within the chamber were tested using broad-band sound, 100Hz-40kHz. Spectral analyses of recordings from 4 positions are shown in Figure 2.1, together with the resultant ratio of two of the spectra. At no frequency did recorded sound pressure levels at points equidistant from the sound source differ by more than -+3dB. Echo levels within the chamber had previously been shown to be more than 40dB below signal level (Hutchings (1981)).

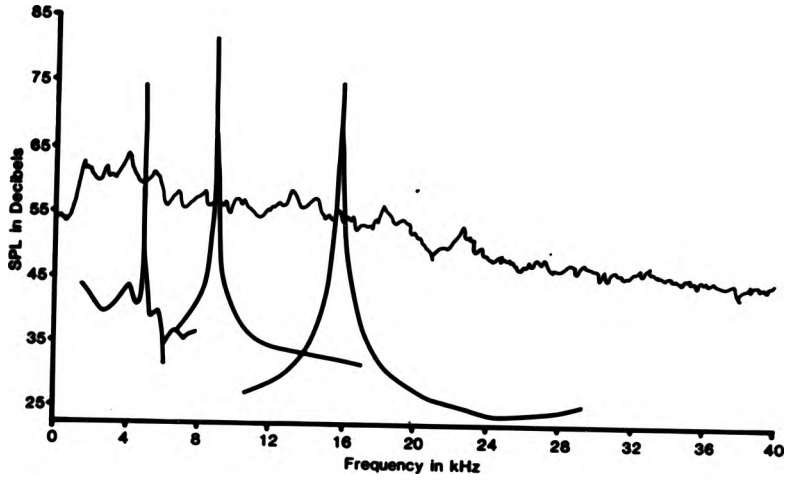
2.3. Sound Production.

The signals used were either pure tones or continuous broad-band sound. The pure tones were produced on a Phillips Type GM 2137 signal generator and the broad-band sound on a Neurolog type NL 754 signal generator. The signals were passed through a Hatfield attenuator type 2125 and amplified by a Xelex 2 x 50watt power amplifier. An Audax TW8B 8ohm loudspeaker was used initially, but for later work a Technics leaf tweeter type DF05 was used. Spectra from the latter are shown in Figure 2.1. A spectrum from the former is shown in Figure 2.2 together with sample spectra of the pure tones used.

The loudspeakers were clamped to a steel arc of 1m radius which could be rotated horizontally (i.e. with the axis of rotation vertical) within the test chamber. The rotation of the arc could be controlled manually from outside the

Figure 2.2: Broad-band and pure tone spectra recorded 1m from the loudspeaker (Audax TW8B) using a B & K microphone, type 4135. The incomplete pure tone spectra have been superimposed on the broad-band spectrum. All spectra are averages of 32 samples and are corrected (adjusted to take into account the microphone correction factor).

Fig. 2.2


85
75
65
55
45
35
25
SPL in Decibels
0
4
8
12
16
20
24
28
32
36
40
Frequency in kHz

chamber by means of a system of cogwheels and chain, the precise position of the arc being monitored on a 360° angle indicator. The vertical position of the loudspeakers could be changed by moving them manually up and down the arc.

2.4. Animal Preparation.

The experimental subjects were weighed prior to anaesthesia or sacrifice, and measurements of the size and natural position (in rats and guinea pigs) of the pinnae made. Sacrifice was carried out either by intravenous injection of sodium pentobarbitone or by chloroforming. Details of the anaesthetics used are given below.

Early experiments were carried out on New Zealand White rabbits using cadavers or cadaver heads. Bruel and Kjaer probe microphone types 4135 (1/4in.) or 4138 (1/8in.) were implanted in either the tympanic bulla or the base of the ear canal in the position previously occupied by the TM and acoustically sealed using "Vaseline". In every case, the microphone membrane was protected by a sleeve of polythene which extended 2-3mm past the membrane guard. In some cases, a narrower polythene tube was inserted into the sleeve in order to avoid stretching the base of the ear canal when the 1/4 inch microphone was being used. Exposure of the tympanic bulla involved removal of the angle of the jaw and associated musculature. Entry into the bulla required the use of a dental drill in older rabbits but could be effected with a scalpel point in younger animals.

Substituting a probe microphone for the TM is likely to change the acoustic impedance of the termination of the canal and give overestimates of HRTF amplitudes. When a probe tube of sufficient sensitivity and range became available, it was decided to re-investigate the bioacoustics of the rabbit external ear. The probe (1mm internal diameter) was implanted through a small hole in the tympanic bulla so that the tip was level with the internal wall of the tympanic cavity directly opposite the pars flaccida of the TM. Acoustic sealing of the probe tip was effected with cyanoacrylic cement (Permabond 910) applied around the entry point of the probe. "Vaseline" was then applied to the dissected area to ensure an effective acoustic seal.

The availability of a suitable probe also facilitated biophysical studies of the guinea pig and rat external ears. Probes were implanted in two positions in the guinea pig. In 3 preparations the probe was implanted through the side wall of the ear canal. The probe tip was positioned about 3mm above the TM in these preparations. In 3 other preparations, the probe was implanted through the wall of the tympanic bulla. The probe tip in these preparations was level with the internal wall of the tympanic cavity and was within 1mm of the TM.

Probe implantation in the rat was made through the side of the ear canal because of the small size of the cavity housing the TM. The probe tip was about 2mm above the manubrium in these preparations. Acoustic sealing of the

probe tip was also effected with cyanoacrylic cement and "Vaseline" in both rat and guinea pig preparations.

When rabbits and anaesthetised guinea pigs were used the head was screw mounted to a minimal head holder. An area of skin over the coronal suture was removed and a hole drilled through the exposed skull. The head-holder was a metal rod in the shape of a question mark extending around the tip of the animal's snout before curving downwards and then backwards to fasten to a Leitz ball and socket joint. This, in turn, was attached to a magnetic-based clamp. When rats and guinea pig cadavers were used, the head was mounted in a natural position by resting the lower jaw on a small block of plasticene. All experimental subjects were strapped to a small perspex support platform, tailored to each species used. This was also attached to the magnetic base.

Animals were prepared and mounted outside the test chamber on a laboratory bench. When ready, the animal and its support platform were placed on a steel pedestal positioned centrally in the test chamber. In all cases the subject's head was positioned with the aid of a plumb bob so that the mid-point of the inter-aural axis was over the centre of the pedestal, which was the axis of rotation of the steel arc carrying the loudspeakers. The median sagittal plane of the animal's head was aligned with the steel arc positioned at 0° azimuth on the angle indicator outside the chamber. When rabbits were used the pinnae were held upright in an "alert" position by means of fine wires

hooked through their tips. Television recordings of wild and wild type rabbits in their natural environment had previously been made in order to ascertain natural pinna positions. Observations on guinea pigs and albino rats were made in the animal house at the City of London Polytechnic in order to assess the pinna positions adopted by these species.

The detailed position of the recorded pinna was monitored using a spirit level and protractor to determine the long plane of the pinna opening. The horizontal plane of the pinna opening was determined by placing a ruler horizontally across the widest part of the opening and lining up the rotateable steel arc with the ruler. The azimuthal axis of the pinna opening was then stated to be at 90° to that plane.

Cochlear microphonics were successfully recorded from pigmented guinea pigs, Sprague-Dawley albino rats and New Zealand White rabbits. Anaesthesia and surgery on the first 8 guinea pigs studied were carried out by Dr. A. Palmer.

a) Guinea pigs: young animals weighing between 200gm and 300gm were anaesthetised with a neuroleptic technique which involved pre-medication with 0.18mg of atropine sulphate (sub-cutaneous) followed by an intra-peritoneal injection of 30mg/Kg sodium barbitone. Once comatose, the guinea pigs received intra-peritoneally 4mg/Kg Droleptan (a hypnotic) and 1mg/Kg Operidine (a neuroleptic). Supplementary doses of Operidine (intra-muscularly) and sodium pentobarbitone (0.2 to 0.4 of the induction dose) were given as required.

usually every 1-2 hours.

The subject's core temperature was maintained using a thermostatically controlled heating blanket. Tracheal cannulation was performed to ensure unrestricted ventilation of the lungs and to facilitate the removal of any mucous build-up in the bronchii. The head was attached to the minimal head-holder described above and the auditory bulla was exposed by removing a flap of skin from the area behind the pinna (usually the left). A scalpel point was used to make a small hole in the posterior wall of the bulla. CM potentials were recorded with teflon coated stainless steel wire located on the bony rim of the round window. The wire was held in place with dental cement which also served to reseal the bulla. A small bore nylon tube was incorporated with the recording wire when resealing the bulla. This allowed of pressure equalisation without compromising the closed bulla recording conditions. An indifferent electrode was inserted into the neck musculature and the pinna was repositioned normally using cyanoacrylic cement. The preparation was then transferred to the test chamber as described above.

b) Rabbits: New Zealand white rabbits weighing between 1.9Kgm and 3.6Kgm were anaesthetised with intra-peritoneal injections of 1gm/Kgm urethane followed by smaller supplementary doses when necessary. Similar surgical procedures to those described for the guinea pig were followed except that no tracheal cannulation proved necessary. A heating blanket was not used. Access into the

bulla required the use of a dental drill in older, larger specimens and a silver recording electrode was used. Greater use of cautery was necessary when operating on the rabbit ear, and, in most cases, several branches of the jugular vein had to be ligatured.

c)Rats: Sprague-Dawley albino rats weighing between 315gm and 475gm were anaesthetised with 1ml/Kgm intra-peritoneal Sagatal (a sodium pentobarbitone preparation), followed by smaller supplementary doses when necessary. A similar procedure to that described for the guinea pig was followed except that a heating blanket was not used. The recording electrode was of fine platinum wire. Direct access to the round window was prevented by a bony ridge along which a blood vessel ran and the recording electrode had to be hooked over this ridge and thence onto the round window. The bulla was resealed with cyanoacrylic cement but a fine bore pressure equalising tube was not incorporated in this process.

All animals were sacrificed by an overdose of anaesthetic as soon as data collection was complete. In a number of cases, a biophysical investigation of the recorded ear was then made. When possible, endocasts of the recorded pinna were also made.

2.5. Recording and Analysis.

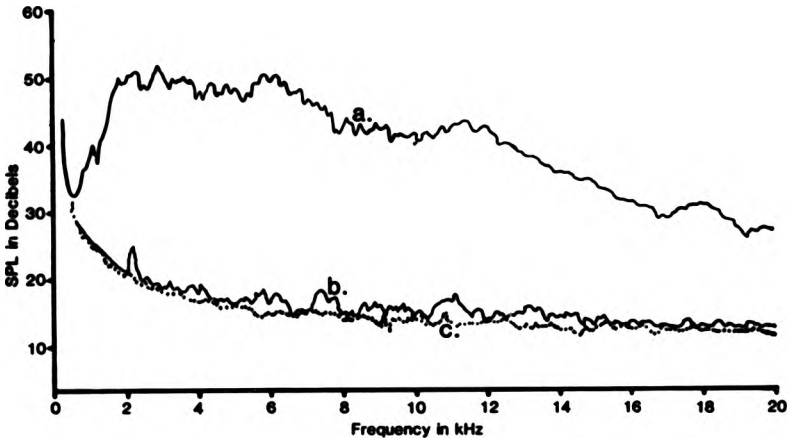
As stated above, in earlier studies on the rabbit external ear, probe microphones were implanted directly into the base of the ear canal. In later work, however,

recordings were made using a probe implanted through the wall of the ear canal. Several attempts were made to build a probe small enough to insert into the ear canals of animals such as the laboratory rat. Conventional probe designs proved inadequate because of standing waves and high frequency attenuation. A design that did prove satisfactory, however, was suggested by the technical division of Bruel and Kjaer, England. This consisted of a 3m long polythene tube of internal diameter 1mm open at both ends with the microphone monitoring SPL's "within" the tube. In order to do this, a steel cap was built which screwed tightly and closely onto a Bruel and Kjaer type 4135 microphone such that the volume of air enclosed above the microphone membrane was minimised. The polythene tube was let into and out of the cap by means of two small apertures. Araldite was used to seal the polythene tubes into the cap and plumbers tape was used to seal the cap to the microphone. Experimentation revealed that the best compromise between high frequency attenuation and resonance was achieved with a tube of about 25cm (the "insert") entering the cap and a tube of 275cm, or more, leaving the cap. This arrangement results in very little resonance above 50Hz (the lower limit of the high resolution signal analyser) and sensitivity over an extensive frequency range is retained (see Fig.2.3)

At the start of biophysical investigations SPL's were recorded from the centre of the test chamber with no animal

Figure 2.3: Spectra from 3m probe, (a) open, (b) blocked, and (c) open, but with signal attenuated by 85dB. Spectra are corrected and are averages of 32 samples.

Fig. 2.3


60
50
40
30
20
10
SPL in Decibels
a.
b.
c.
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz

present. In the case of experiments involving the use of the high resolution signal analyser, the "free field" spectrum was stored in memory. The microphone used to make these recordings was fitted with the polythene sleeve or probe that would be used in that experiment, so that accurate HRTF's could later be calculated. On subsequent placement of the experimental preparation in the test chamber HRTF's could then be obtained from the ratio of the implant : free field spectrum.

HRTF's were obtained for every 10°, 15° or 20° in the azimuthal plane and every 15° or 20° from -40° to +40° or more in the vertical planes. The sound source was thus being located on the surface of an imaginary sphere with the animal's head positioned at the centre of the sphere. As a matter of convention, 0° azimuth was always rostral on the mid-sagittal plane through the head, 90° was ipsilateral to the recorded ear, and hence 180° was caudal on the mid-sagittal plane and 270° was contralateral to the recorded ear. 0° elevation was the horizontal plane grazing the dorsal surface of the head. Planes above this level were designated positive, planes below, negative. Any position on the imaginary sphere could thus be unambiguously specified in terms of its angle of azimuth and angle of elevation.

Pure tone SPL's were monitored outside the test chamber using a B & K frequency analyser type 2107 in conjunction with a B & K band pass filter set type 1612. In early experiments, SPL's were recorded onto polar plot paper

directly from a B & K level recorder type 2305, but this methodology was quickly superceded by the use of broad band sound and high resolution signal analysis using a B & K high resolution signal analyser type 2033. This machine resolves into 50Hz bins from 50Hz-20kHz thus giving far more detail than would be possible with conventional pure tone analysis. Tape recording of microphone input and replaying at half speed into the signal analyser allowed analysis of the broad band sound in 100Hz bins from 100Hz-40kHz. Tape recording was done on a Racal Store 7 instrumentation recorder at 60ips or 30ips. Averages of 32 samples were always used to obtain HRTF's or other functions. IID spectra were obtained by storing the average of 32 samples recorded with the sound source at a particular contralateral position and then obtaining the average of 32 samples from the relevant mirror-image ipsilateral position, the ratio of the two averaged spectra then giving the IID spectrum. Thus, for say an IID spectrum for 30° azimuth,0° elevation, the required ratio would be for 30° : 330° azimuth (both at 0° elevation). IID spectra were obtained for the same range of sound source positions as for HRTF's. The various spectra obtained with the signal analyser were plotted directly onto graph paper using a Gould X-Y recorder type 3054. Calibration of the plots was then carried out by using the analyser cursor to determine the amplitude of some of the spectral features and noting the measurements.

CM potentials were amplified (x100) with an A.C.

preamplifier and headstage (NL 103). Filtering was carried out with a Neurolog type NL125 filter, the low frequency filter being set at 5Hz and the high frequency filter at 50kHz. The 50Hz notch was "in". Further amplification (up to x20) was carried out using a Neurolog type NL 105 amplifier. CM's were monitored on an oscilloscope and recorded using an instrumentation recorder (Racal Store 7). The relationships between CM amplitudes and signal SPL's were obtained for a range of pure tones for each preparation in order to determine the "dynamic range" of the CM. Signal SPL's were then set within the "dynamic range". In rabbit and rat studies CM amplitude functions were also obtained using broad-band sound and high resolution signal analysis. This was not done in the CM studies on guinea pigs, however. Recordings were subsequently analysed using the high resolution signal analyser in the manner described above.

Interaural phase differences as functions of azimuth were obtained during both CM and biophysical studies by monitoring changes in phase angle with changes in sound source position. A B & K phase meter type 2971, using signal source as reference, was employed for this. A range of pure tones was used and phase angle measurements for every 10° or 20° azimuth were made.

The stability of both CM and probe implant preparations was monitored during the course of each experiment by obtaining spectra from the same loudspeaker position at various time intervals throughout the experiment.

2.6. Experimental Modifications of the External Ear.

Most of the experiments involving modification to the external ear were performed on cadavers. The exceptions to this were the guinea pig where enlargement of the tragal notch or removal of the pinna were performed during CM recording experiments; and the rat and the rabbit, when simple bridging of the tragal notch was performed using "Vaseline". Modifications to cadavers included removal of whole or part of the pinna, and blocking the meatus, tragal notch or fossa with plasticene. In addition, puncturing or stiffening of the TM were performed, the former by inserting a wire into the meatus, the latter by either injecting water into the bulla or by coating the middle-ear side with Permabond 910 glue, followed by resealing of the bulla. In 3 of the rabbit biophysical studies the effective length of the meatus was altered in order to study axial resonance within the meatus. These alterations were effected by gluing a polythene tube into the meatus and placing the microphone at various positions within the tube.

2.7. Endocasts.

Endocasts of the external ears of experimental subjects were made by moulding plasticene supports for the pinna,

arranging the head and pinna so that the pinna opening was horizontal, and then filling the whole of the external ear with liquid casting plaster or silicon moulding rubber (Silastic E). Removal of the hardened cast one or two days later produced an accurate copy of the interior of the pinna but because of the sharp bend in, and expansion of, the proximal end of the ear canal in most specimens a complete cast of the ear canal was obtained only when silicon moulding rubber was used. This therefore became the preferred moulding material and all measurements of ear canal dimensions have been obtained from silicon moulding rubber endocasts.

2.8. Modelling.

Simple plasticene and polythene models were constructed in order to ascertain the physical causes of some of the major acoustical effects of the external ears under investigation. The models were generally simple geometric shapes such as cylinders and cones but attempts were also made to replicate some specimens more accurately. The acoustics of the models were investigated using the probe and techniques of analysis described above.

2.9. Concluding Remarks.

Minor variations in technique and experimental procedure necessitated by differences between the species of animal under investigation are described in the chapters devoted to each species.

Throughout this study, sound pressure levels (SPL's) are re 20uPa. The term "intensity" has been retained in phrases such as "interaural intensity difference" because of its common use in this field. This phrase actually refers to the interaural level difference.

CHAPTER 3. RESULTS: THE RABBIT

3.1. Behavioural Observations.

Approximately 12 hours of observation on the pinna postures of wild rabbits were carried out in the grounds of King's College Field Centre, Rogate, Hamps. and in the South Weald, Brentwood, Essex, during the summer and autumn of 1980. Video recordings were made with a Sony field T.V. camera and recorder. Further observations and recordings (8 hours) were made on a wild type pet rabbit in a Brentwood garden in July, 1981.

All of the observed rabbits showed 2 basic pinna postures: 1) where the pinnae were layed back on the head in a relaxed position and 2) where the pinnae were held erect in an "alert" posture. In the alert position the pinnae were held with the longitudinal plane of the opening at between about 15° and 20° to the vertical, and typically with the two pinnae symmetrically orientated (see Fig.3.1.) With one exception, the wild rabbits orientated the pinnae to the front for more than 50% of the time. The one exception was a solitary individual observed while feeding facing its burrow. This animal held its pinnae orientated to the rear continously. The pinnae could also be held asymmetrically when in the alert position, and one or both pinnae could be moved in "azimuthal sweeps" of varying magnitude. Asymmetrical postures were rarely seen in the wild rabbits but were common in the pet rabbit that was observed. A likely explanation of this is that the fine movements and slight asymmetries were not discernible at

Figure 3.1: Symmetrical alert pinna postures of the rabbit:

(a) front orientated.

(b) rear orientated.

Fig. 3.1

the distances from which the wild rabbits were observed.

There is clearly no one, set, pinna position adopted by the rabbit; each individual presumably employs the pinna postures and movements that are appropriate to the monitoring of its environment at that particular moment. It was therefore decided to hold the pinnae "erect" (around 15° to the vertical) but to allow the "recorded" pinna to face whatever angle of azimuth it naturally tended towards. Forcing the recorded pinna to face a previously set angle of azimuth compresses the pinna volume and is therefore undesirable in any case. In fact, the pinnae of the anaesthetised or freshly sacrificed rabbits tended to face the anterior/lateral quadrant.

3.2. Directional Characteristics of the External Ear.

Azimuthal dependence functions were obtained from 6 cadaver heads using pure tones ranging from 1kHz to 40kHz. SPL's were monitored for every 10° or 15° azimuth using 1/8 inch or 1/4 inch B & K microphones implanted into the wall of the tympanic bulla or into the base of the meatus.

A B & K level recorder was used to measure SPL's as described in Chapter 2. A typical set of azimuthal dependence functions is shown in Fig.3.2. It can be seen that directional sensitivity increases markedly above 4kHz, increasing generally with frequency thereafter, although at some of the higher frequencies, e.g. 25kHz and 40kHz, the main lobes of the functions are not well developed. The acoustic axis of the pinna, as defined by the angle of

Figure 3.2: Azimuthal dependence functions at 0° elevation obtained using pure tones. (From MG12(a), cadaver head, 1/8 inch microphone in wall of tympanic bulla, right pinna facing 45° azimuth.) The functions are adjusted to 0 dB at 0° azimuth.

Fig. 3.2

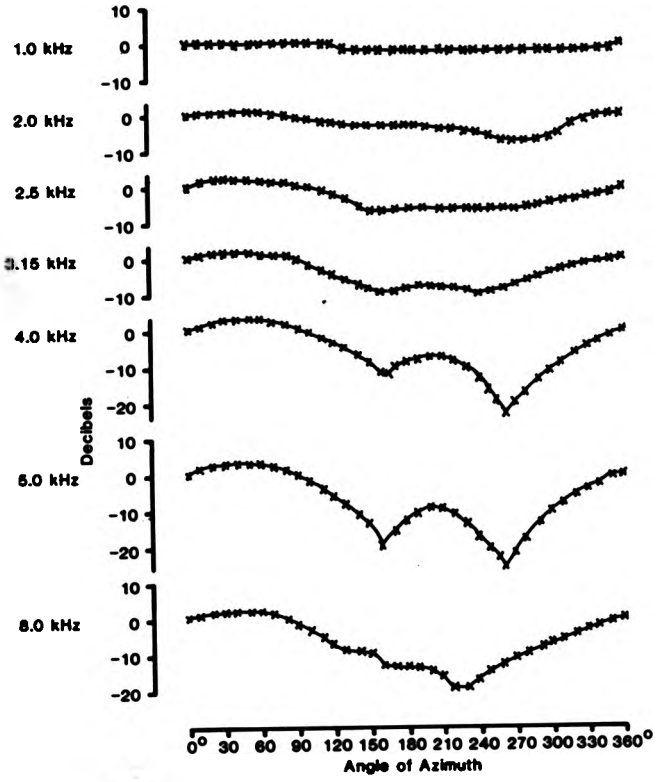
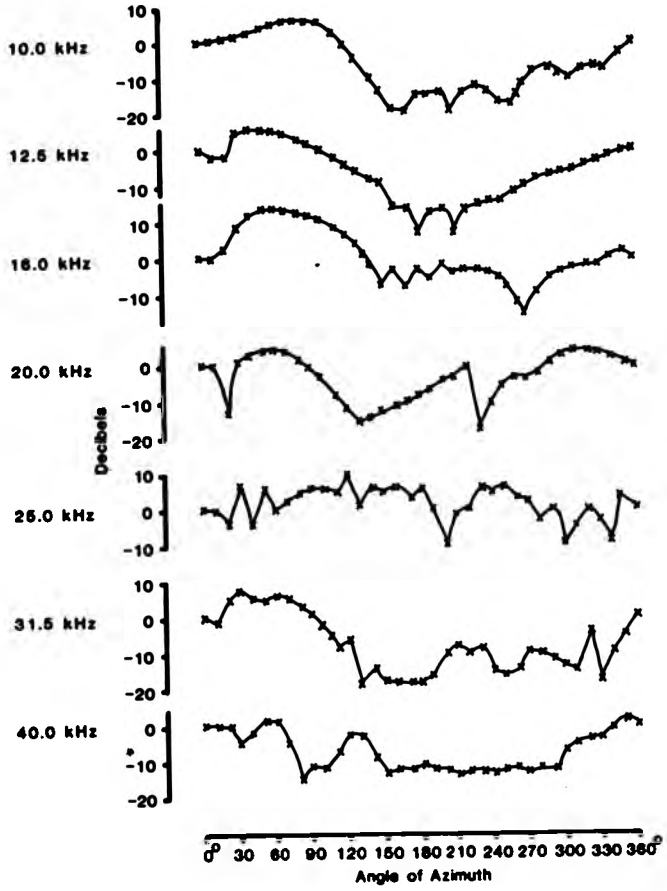

1.0 kHz
2.0 kHz
2.5 kHz
3.15 kHz
4.0 kHz
5.0 kHz
8.0 kHz
10
0
-10
-20
Decibels
0° 30 60 90 120 150 180 210 240 270 300 330 360°
Angle of Azimuth

Fig. 3.2 cont'd.


10.0 kHz
12.5 kHz
16.0 kHz
20.0 kHz
25.0 kHz
31.5 kHz
40.0 kHz
10
0
-10
-20
Decibels
0° 30 60 90 120 150 180 210 240 270 300 330 360°
Angle of Azimuth

azimuth at which SPL's are maximal, is generally posterior to the angle of azimuth faced by the pinna opening (45° for the data-set in Fig. 3.2). This is probably explained by the asymmetry of the rabbit pinna in cross section (see Fig.4.1). The acoustic axis changes slightly with frequency (compare the functions at 10kHz and 12.5kHz, Fig.3.2) as do the azimuthal positions of the minima or "nulls".

The directional characteristics of 4 external ears are presented in Fig.3.3 as functions of frequency. The -3dB acceptance angle (the angle of azimuth spanned by the -3dB points on either side of the maximum point in the azimuthal dependence function) has been chosen as a convenient measure of directionality as it is often used to compare directional devices (Beranek 1954). The general increase in directionality with frequency is clear. An alternative method of representing directionality would be in terms of the greatest difference in SPL at a given frequency, i.e. as maximal directionality. This has not been done here as the value or "depth" of the null(s) in the azimuthal dependence function is often a major contributor to the maximum directionality. Null values often depend on signal to noise ratios and are therefore too variable from experiment to experiment to provide a satisfactory basis for comparison.

Reorientation of the pinna during pure tone azimuthal dependence measurements was carried out on 4 occasions by pulling on the base of the pinna with Selotape. This resulted in some compression of the pinna volume but the

effects on the acoustic orientation of the external ear are clear (Fig.3.4): reorientation of the recorded pinna by approximately 40° results in a 30° shift in the acoustic axis. The 10° discrepancy occurred on all 4 occasions that this modification was made and is suspected to be the result of the change in pinna volume. Casual observations of pinnae where severe compression occurred revealed strong shifts in acoustic axis as a consequence of the compression. It should be noted that not only the main lobe of the azimuthal dependence functions but also the nulls shift with pinna reorientation (Fig.3.4).

The effects of pinna removal were assessed on 4 occasions using the same recording methods as above. The pinna was removed by cutting through the base of the concha to leave the meatus opening directly onto the surface of the head. The contribution of the pinna to azimuthal dependence patterns was then obtained from the ratio of SPL, pinna intact: SPL, pinna removed for every 15° azimuth at selected frequencies. Results for one animal are shown in Fig.3.5: the acoustic axis is at about 90° and it can be seen that the directivity pattern of each function is very largely the result of the action of the pinna on the sound field. The shape of the main lobe is similar for the two functions at all frequencies: discrepancies between the two functions in the posterior (180°) and contralateral (270°) angles of azimuth may be the result of head "shadow" effects. This is discussed in Chapter 4.

Figure 3.3: -3dB acceptance angles plotted as functions of frequency for 4 rabbits, from The main lobes of their azimuthal dependence functions.

Figure 3.4: Azimuthal dependence functions at 0° elevation obtained using pure tones:
x------x pinna facing 60° azimuth,
o------o pinna facing 20° azimuth. (From MGB1, cadaver head, 1/8 inch microphone in base of left meatus.)

Fig. 3.3

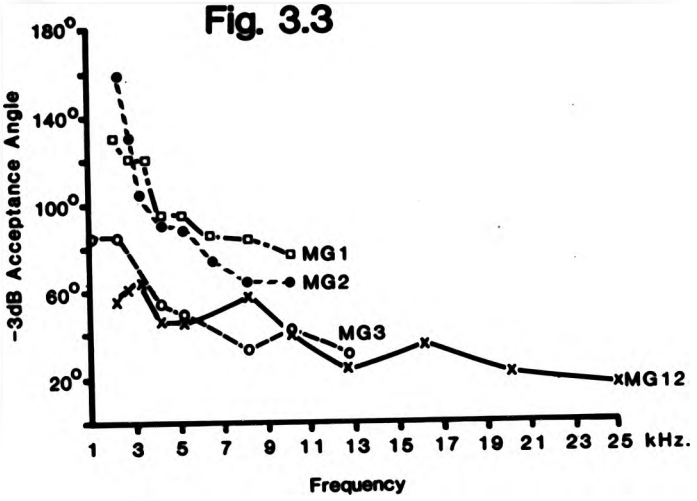

180°
140°
100°
60°
20°
-3dB Acceptance Angle
MG1
MG2
MG3
xMG12
1 3 5 7 9 11 13 15 17 19 21 23 25 kHz.
Frequency

Fig. 3.4

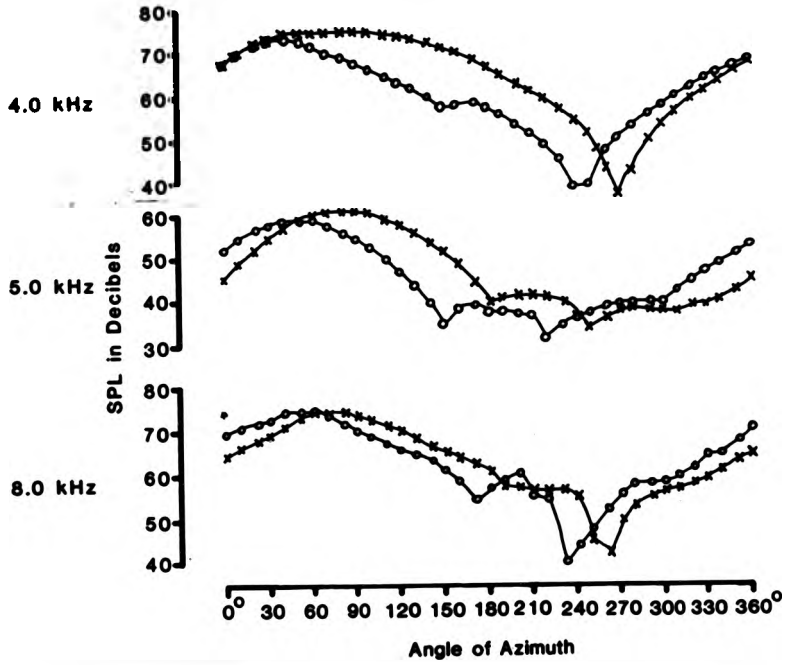

4.0 kHz
5.0 kHz
8.0 kHz
SPL in Decibels
80
70
60
50
40
60
50
40
30
80
70
60
50
40
0° 30 60 90 120 150 180 210 240 270 300 330 360°
Angle of Azimuth

Figure 3.5: Azimuthal dependence functions at 0° elevation obtained using pure tones: x_____x intact ear, o.....o ratio of pinna intact : pinna removed. (From MG1 cadaver head, 1/8 inch microphone in base of right meatus.) The functions are adjusted to 0 dB at 90° azimuth.

Fig. 3.5

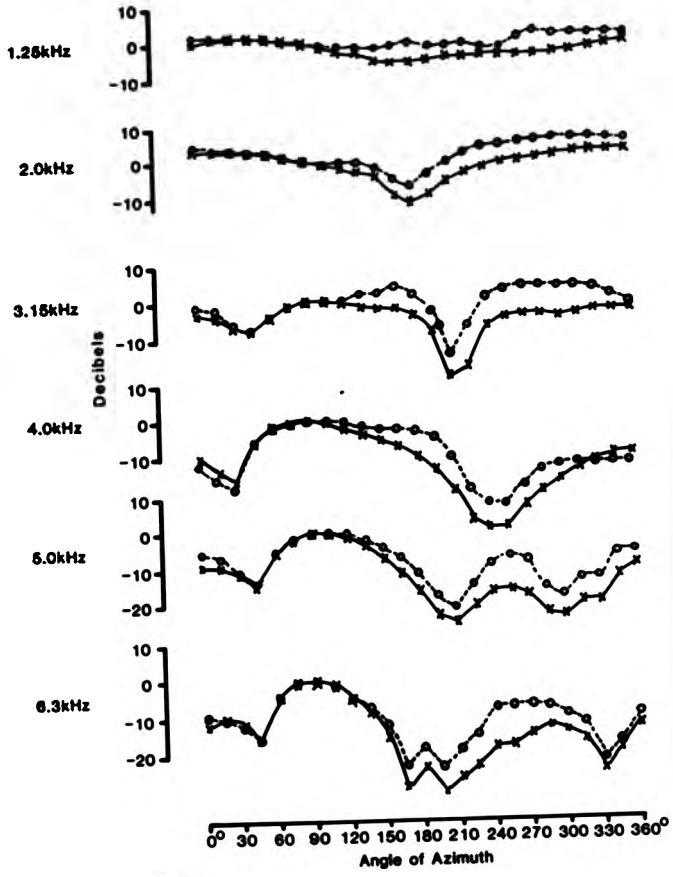
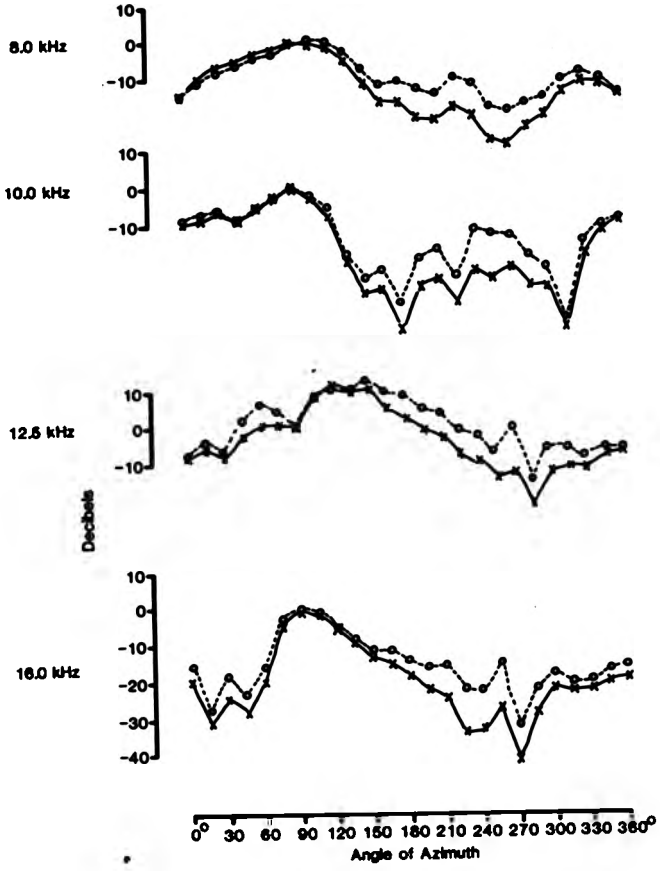

1.25kHz
2.0kHz
3.15kHz
4.0kHz
5.0kHz
6.3kHz
10
0
-10
-20
Decibels
0° 30 60 90 120 150 180 210 240 270 300 330 360°
Angle of Azimuth

Fig. 3.5 cont'd.


8.0 kHz
10.0 kHz
12.5 kHz
16.0 kHz
10
0
-10
-20
-30
-40
Decibels
0° 30 60 90 120 150 180 210 240 270 300 330 360°
Angle of Azimuth

3.3. Head Related Transfer Functions (HRTF's).

An alternative method of assessing the directional characteristics of the external ear is to compare HRTF's obtained from different sound source positions. This method has the advantage of representing a complex sound as one function in the frequency/intensity domain and hence might be said to represent what the animal actually hears at any one moment. A series of HRTF's from an anaesthetised rabbit is shown in Fig.3.6. The HRTF's are the ratio of the stored "free-field" spectrum to the spectrum obtained when the probe was implanted into the tympanic cavity. Broad-band sound and high resolution signal analysis were used as described in Chapter 2. At 0° elevation, greatest overall gain is shown between 40° and 60° azimuth (Fig.3.6(a)). The recorded pinna was facing 25° azimuth. Noteworthy features of this family of HRTF's are the sharp peak of up to 26dB at 2.1kHz, a second peak at 3.4kHz, and smaller but consistent peaks at 4.3kHz and 7.7kHz. Only above about 4.8kHz do the anterior-ipsilateral HRTF's (Fig.3.6(a)) start to show directional sensitivity and this does not increase uniformly with frequency; the frequencies at which nulls tend to develop are the most directionally sensitive.

Reference to the posterior-ipsilateral HRTF series at 0° elevation (Fig.3.6(b)) will show that the peak at 2.1kHz is maintained to 17dB or more but that the 3.4kHz peak drops to 10dB at 180° azimuth. This HRTF series shows strong directionality in the 4kHz-6kHz region associated with the establishment of a null at about 6kHz at the more posterior

Figure 3.6: A family of HRTF's (ratio of SPL near the TM : freefield SPL, plotted as a function of frequency) from a living rabbit: (a) anterior/ipsilateral sector, (b) lateral and posterior/ipsilateral sectors, (c) sample contralateral spectra. All at 0° elevation. (From RP9, left pinna facing 25° azimuth, probe in base of left meatus.)

Fig. 3.6

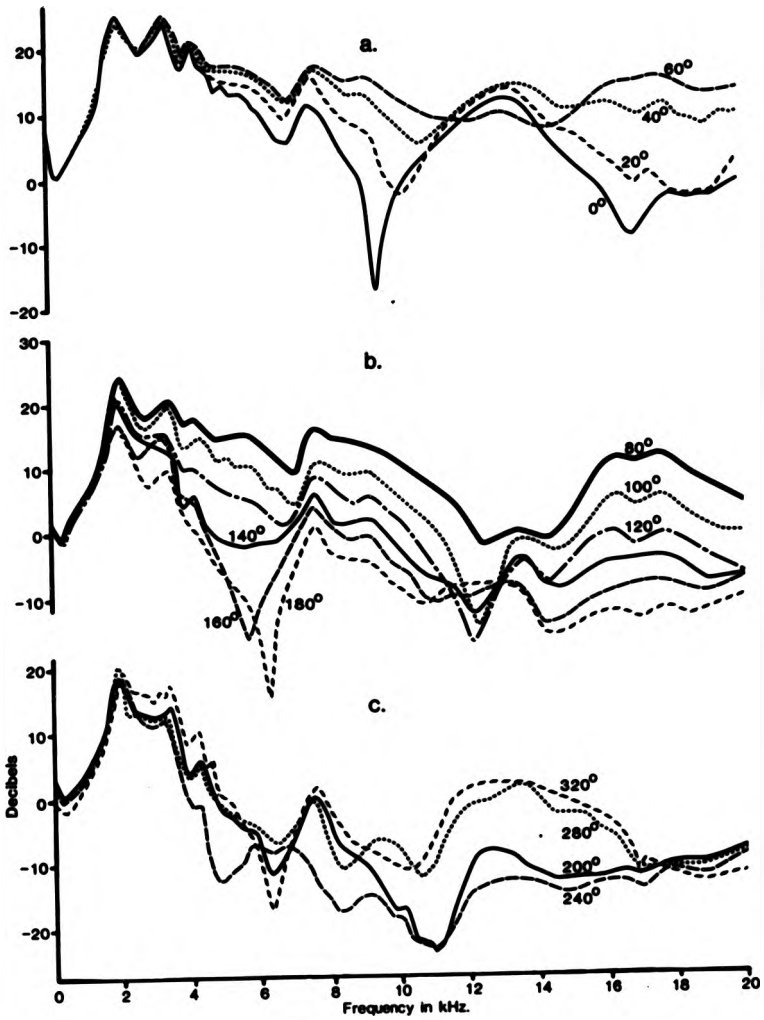

a.
b.
c.
60°
40°
20°
0°
80°
100°
120°
140°
160°
180°
320°
280°
200°
240°
Decibels
Frequency in kHz.

Figure 3.6 (contd.): HRTF's at +40° elevation:

(d) anterior/ipsilateral sector.

(e) posterior/ipsilateral sector.

(f) contralateral sector.

Fig. 3.6 cont'd.

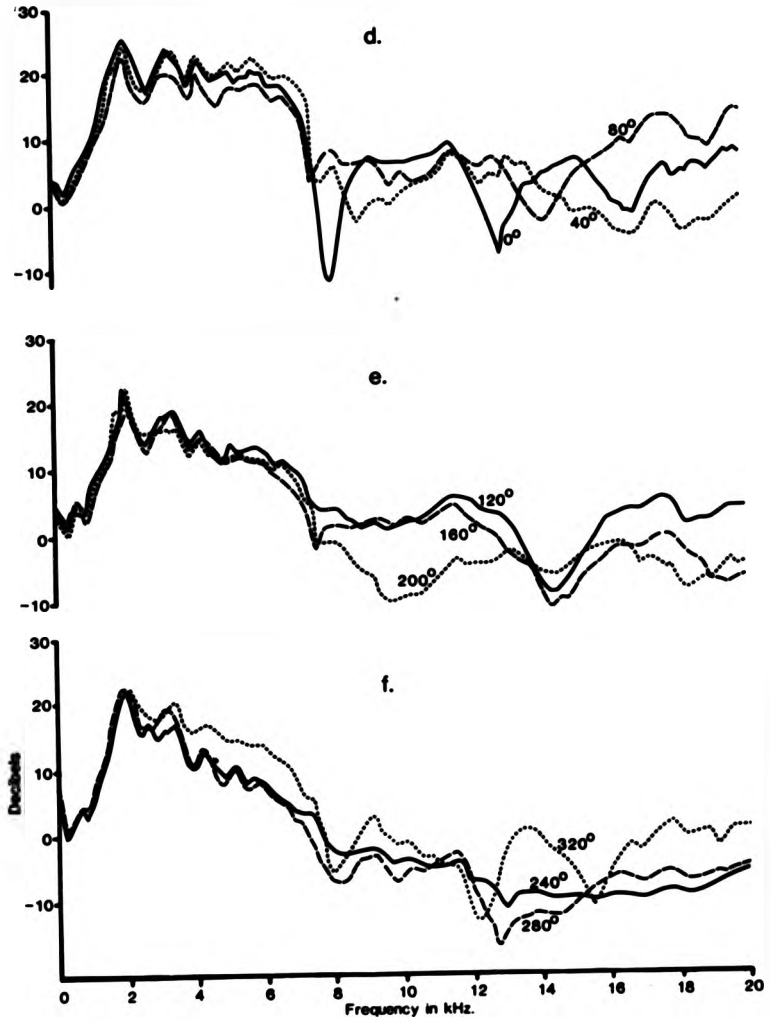

d.
e.
f.
30
20
10
0
-10
80°
40°
0°
120°
160°
200°
320°
240°
280°
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 3.6 (contd.): HRTF's at +20° elevation;

(g) anterior/ipsilateral sector.

(h) posterior/ipsilateral sector.

(i) contralateral sector.

Fig. 3.6 cont'd.

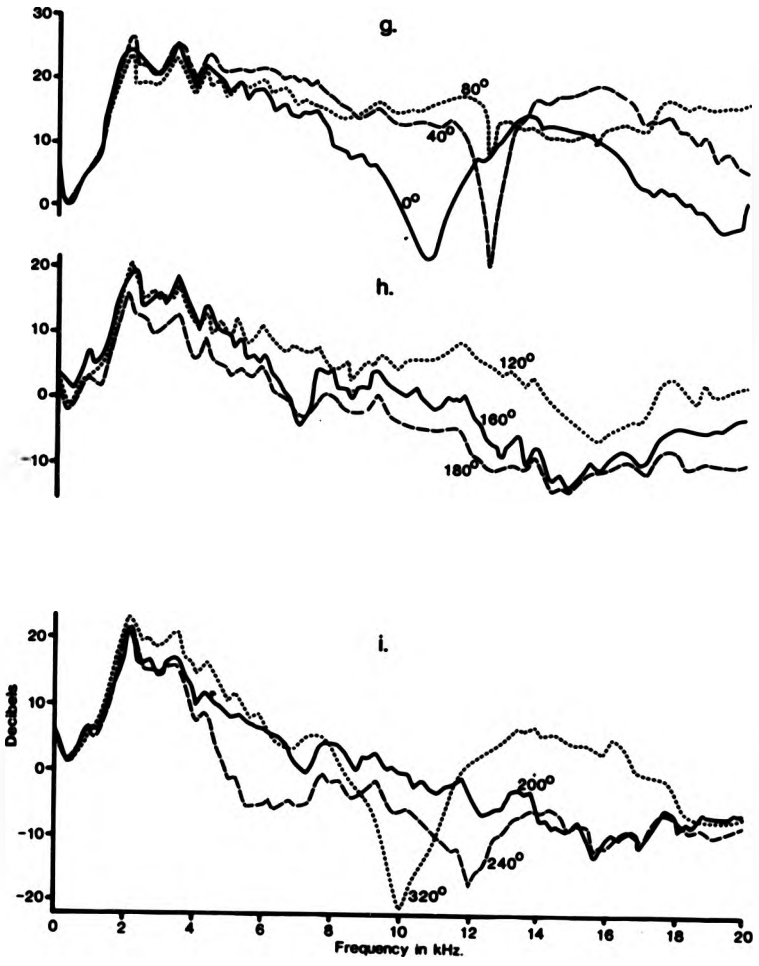

g.
30
20
10
0
80°
40°
0°
h.
20
10
0
-10
120°
160°
180°
i.
20
10
0
-10
-20
Decibels
200°
240°
320°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 3.6 (contd.): HRTF's at -20° elevation:

(j) anterior/ipsilateral sector.

(k) posterior/ipsilateral sector.

Fig. 3.6 cont'd.

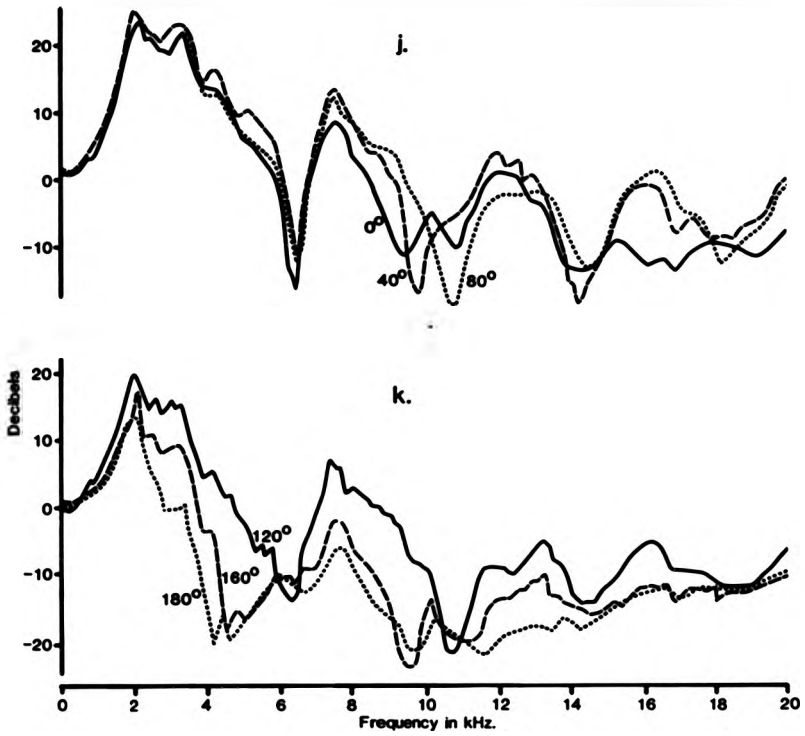
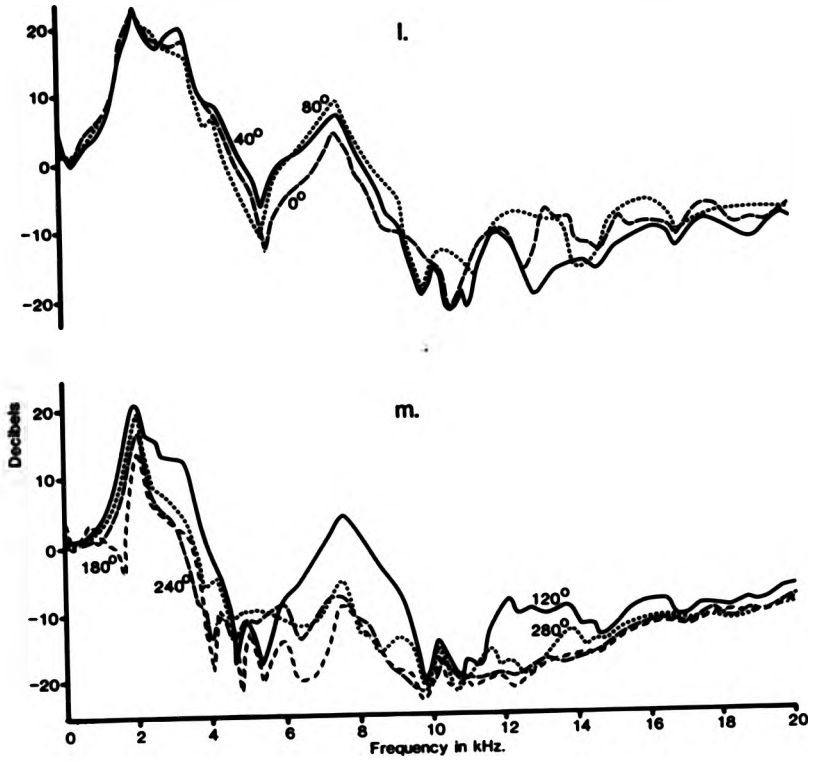

j.
20
10
0
-10
0°
40°
80°
k.
Decibels
20
10
0
-10
-20
120°
160°
180°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 3.6 (contd.): HRTF's at -40° elevation:
(l) anterior/ipsilateral sector.
(m) posterior sector.

Fig. 3.6 cont'd.


l.
20
10
0
-10
-20
40°
80°
0°
m.
Decibels
180°
240°
120°
280°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

angles. Sample HRTF's from the contralateral sector at 0° elevation (Fig.3.6(c)) show further reductions in gain in the 6kHz region and also in the 10kHz-12kHz region where a further set of nulls tends to develop.

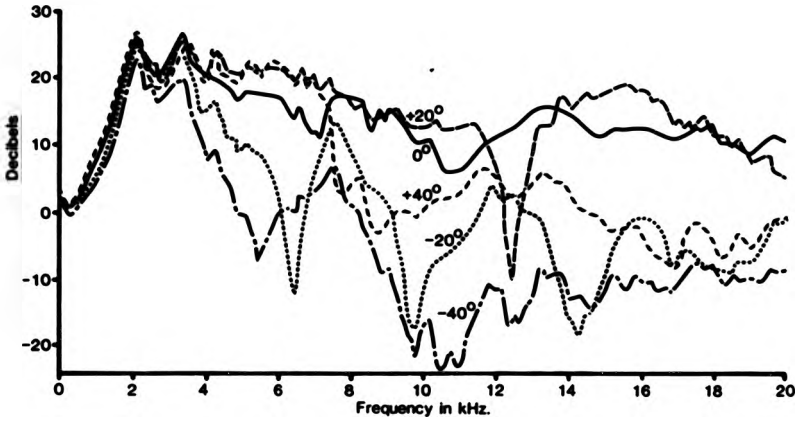
HRTF's at different angles of elevation have distinctive appearances which depend principally on the frequencies at which the nulls occur. Thus at +40° elevation (Fig.3.6(d), (e) and (f)) the first (low frequency) null occurs in the 8kHz region and gain remains high up to 7kHz or so. Similarly at +20° elevation, (Fig.3.6(g), (h) and (i)) although low frequency minima are only apparent at 160° and 180° azimuth (Fig.3.6(h)).

HRTF's at lower angles of elevation show sharp minima at all angles of azimuth. At -20° elevation, (Fig.3.6(j) and (k)), the low frequency nulls appear at about 6.5kHz in the anterior-ipsilateral HRTF's (Fig.3.6(j)) but shift down-frequency to 5kHz or less in the posterior sector (Fig.3.6(k)). The tendency of the nulls to occur at quasi-harmonic intervals is clearly seen in the -20° elevation HRTF's. The nulls in the -40° elevation HRTF's (Fig.3.6(l) and (m)) occur at yet lower frequencies and the loss of gain in the 2.5kHz-4kHz region is severe.

The characteristic appearance of the HRTF's obtained at different angles of elevation of the sound-source is summarised in Fig.3.7. Although sharp low-frequency nulls are not evident at 0° and +20° elevation, these spectra show characteristic differences in the levels of gain in

Figure 3.7: HRTF's from a living rabbit for various angles of elevation at 40° azimuth. (From RP9, probe in base of left meatus, pinna facing 25° azimuth.)

Fig. 3.7

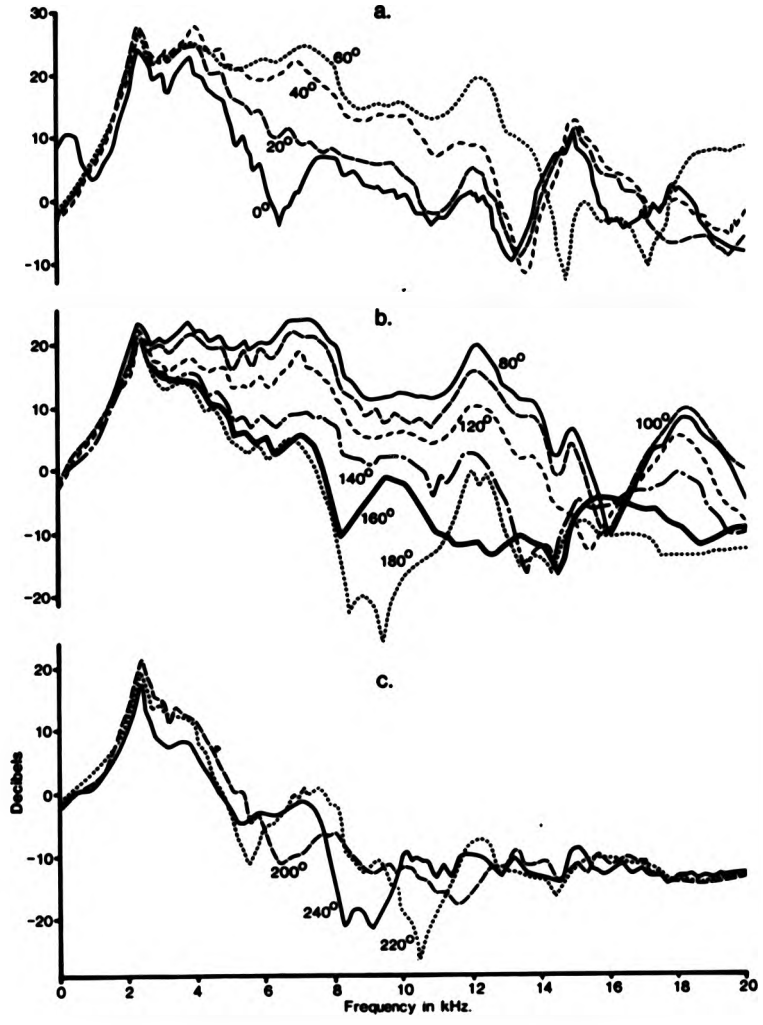

30
20
10
0
-10
-20
Decibels
+20°
0°
+40°
-20°
-40°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

the 4kHz-7kHz range, and from -40° to +20° elevation the spectra are readily distinguishable. Above +20° elevation HRTF's this is not the case (in the low frequency region). The HRTF's in Fig.3.7 were obtained with the sound-source at 40° azimuth. HRTF's obtained from the anterior-ipsilateral sector were generally distinct in their appearance over a range of elevations.

The HRTF's presented in Figs.3.6 and 3.7 are regarded as typical of the New Zealand White rabbit. Potential sources of variation in HRTF's include both natural inter-individual variation and variation in the preparation of the specimen. The state of the animal, i.e. whether living, dead or a severed head, and the position of the probe or microphone in the ear are of particular concern. Both living and dead animals have therefore been investigated using a variety of techniques, including CM recordings. The latter should, in theory, leave the acoustical properties of the external ear unaffected. In order to study inter-individual variation, a standardised technique was developed where the same probe was implanted into fresh cadaver heads in the same position. The probe tip was positioned flush with the internal wall of the ear canal directly opposite the pars flaccida. It was thus close to the intact TM but, because of the relatively high acoustic impedance of the probe tip (1mm diameter) unlikely to greatly affect the acoustical properties of the ear. HRTF's obtained in this series of studies showed the same basic

Figure 3.8: HRTF'S from a cadaver head:
(a) anterior/ipsilateral sector,
(b) lateral and posterior-ipsilateral sector,
(c) samples from the contralateral sector,
all at 0° elevation (From RP4, left pinna facing 26° azimuth. Probe in base of left meatus.)

Fig. 3.8

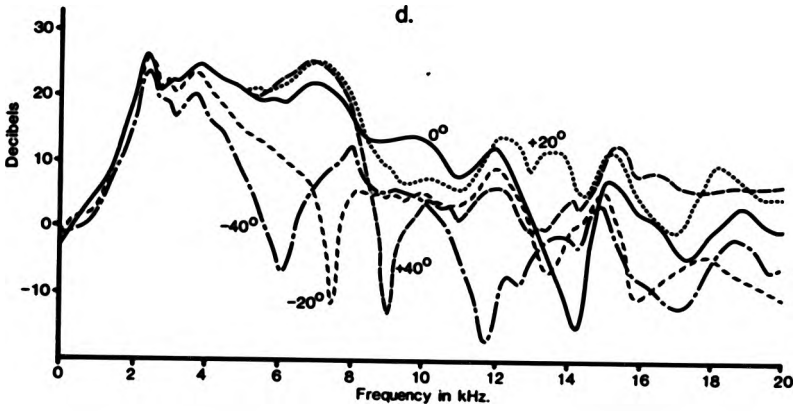

a.
b.
c.
0°
20°
40°
60°
80°
100°
120°
140°
160°
180°
200°
220°
240°
Decibels
Frequency in kHz.

pattern as those shown in Fig.3.6. A sharp peak in the 2kHz region was followed by a second peak around 3.5kHz with nulls and smaller peaks occurring at higher frequencies. The sharpness of the HRTF features and the frequencies at which they occurred varied from preparation to preparation however. Thus RP4 (rabbit probe study number 4) showed a sharp peak of up to 27dB at the relatively high frequency of 2.4kHz and a second peak at 4.0kHz (Fig. 3.8(a), (b), (c) and (d)). The nulls also tended to occur at higher frequencies (about 1kHz higher) than in the RP9 HRTF's (Fig. 3.6). The pinna of RP4 measured 8.5cm in length (pinna tip to base of tragal notch) whereas that of RP9 measured 9.9cm. The 1.4cm difference in pinna length appears to be reflected in a 1.7cm to 2.0cm difference in the wavelengths of the low frequency HRTF peaks and about 0.7cm difference in the wavelengths of the low frequency nulls. It should, of course be remembered that RP9 was alive and hence the air temperature in the ear was likely to have been above room temperature. Slight increases in air temperature would result in slight increases in the speed of sound which would result in slight decreases in the frequencies of standing waves and similar phenomena. These changes are only likely to be of the order of 2% or less however and cannot account for all of the differences between the two animals. The RP4 elevation series of HRTF's at 40° azimuth (Fig.3.8(d)) shows the same up-frequency shift of nulls with increasing elevation as does RP9 (Fig.3.7).

Figure 3.8 (contd.):

(d) HRTF's at 40° azimuth at various elevations (From RP4, left pinna facing 26° azimuth, probe in base of left meatus).

Fig. 3.8 cont'd.


d.
30
20
10
0
-10
Decibels
0°
+20°
-40°
+40°
-20°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

In contrast to RP4, RP8 (Fig.3.9) HRTF's show a blunt peak at 2.0kHz followed by a series of 3 distinct peaks at 3.0kHz, 4.2kHz and 5.3kHz. The anterior-ipsilateral HRTF's (Fig.3.9(a)) are characterised by a series of sharp nulls which tend to occur 1kHz or more lower than their counterparts in the RP4 HRTF's (Fig 3.8). The low frequencies at which the RP8 HRTF features occur can be explained by the relatively large size of the animal (pinna length 10.6cm). The relatively posterior orientation of the pinna face (60° azimuth) also explains the sharpness and number of nulls in the anterior-ipsilateral HRTF's (Fig.3.9(a)). However, the shapes and number of peaks in the HRTF's appear to be idiosyncratic to this animal. It is therefore of interest to examine HRTF's obtained from the other ear (the right) of this animal. These are shown in Fig.3.10. The first 3 peaks occur at the same frequencies as in the left ear (Fig.3.9), but they are sharper, and the fourth peak appears to be at a higher frequency. The peak at 7.8kHz is also unusually distinct. The size, shape and orientation of the left and right pinnae of RP8 were very similar. However, the right-ear recordings were made 24 hours after the left, when rigor-mortis and hardening of the pinnae had set in. The detailed differences in peak shape may therefore reflect more the condition of the preparation than fundamental inter-ear differences. This is discussed further below. The "on-axis" HRTF's at different elevations are shown for the right ear of RP8 in Fig.3.10(d). Inexplicably, and unlike the left-ear HRTF's

Figure 3.9: HRTF's obtained from a cadaver head:
(a) anterior-ipsilateral sector,
(b)posterior-ipsilateral sector,
(c) contralateral sector, all at 0° elevation,
(d) for various elevations at 60° azimuth.
(From RP8, pinna facing 60° azimuth, probe in base of left meatus.)

Fig. 3.9

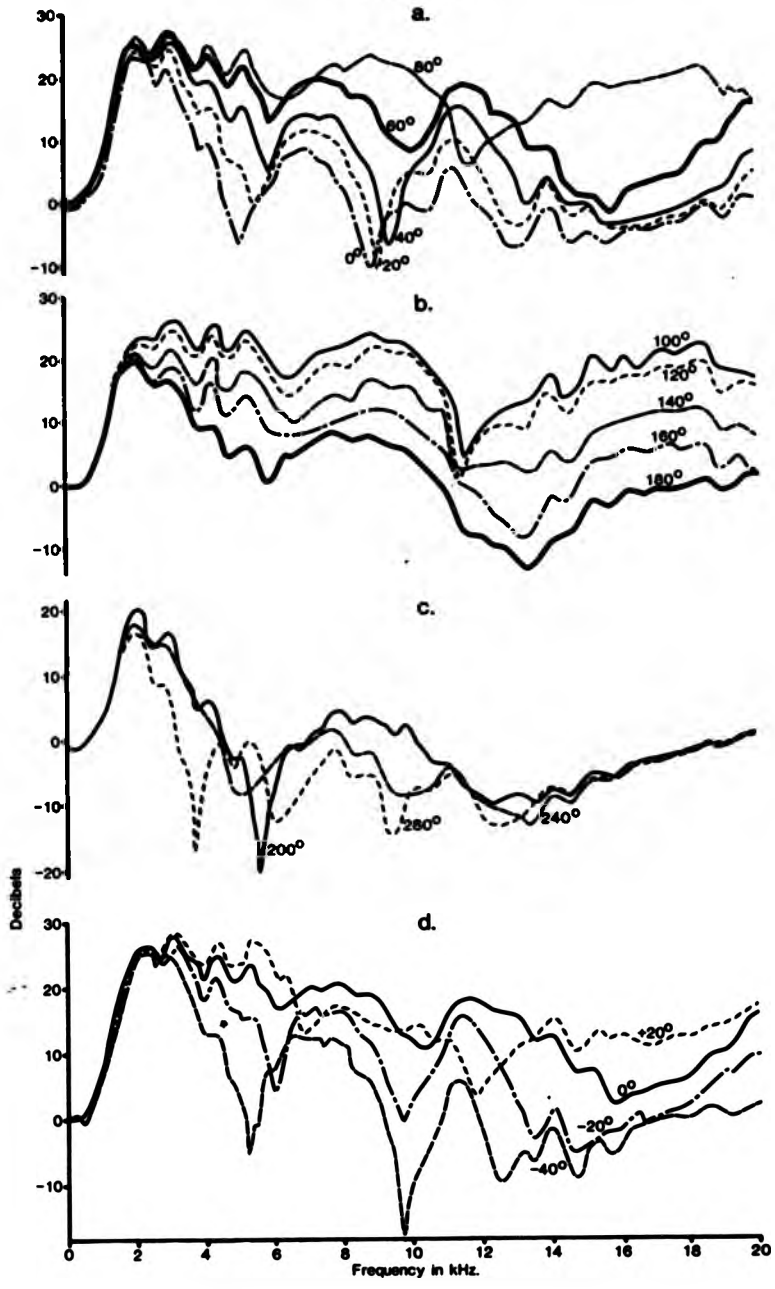

a.
80°
60°
40°
0°
20°
b.
100°
120°
140°
160°
180°
c.
200°
220°
240°
d.
+20°
0°
-20°
-40°
Decibels
Frequency in kHz.

Figure 3.10: HRTF's from cadaver head:

(a) anterior-ipsilateral sector,

(b) lateral and posterior-ipsilateral sector,

(c) contralateral sector, all at 0° elevation,

(d) for various elevations at 80° azimuth.

(From RP8, right pinna facing 72° azimuth,

probe in base of right meatus)

Fig. 3.10

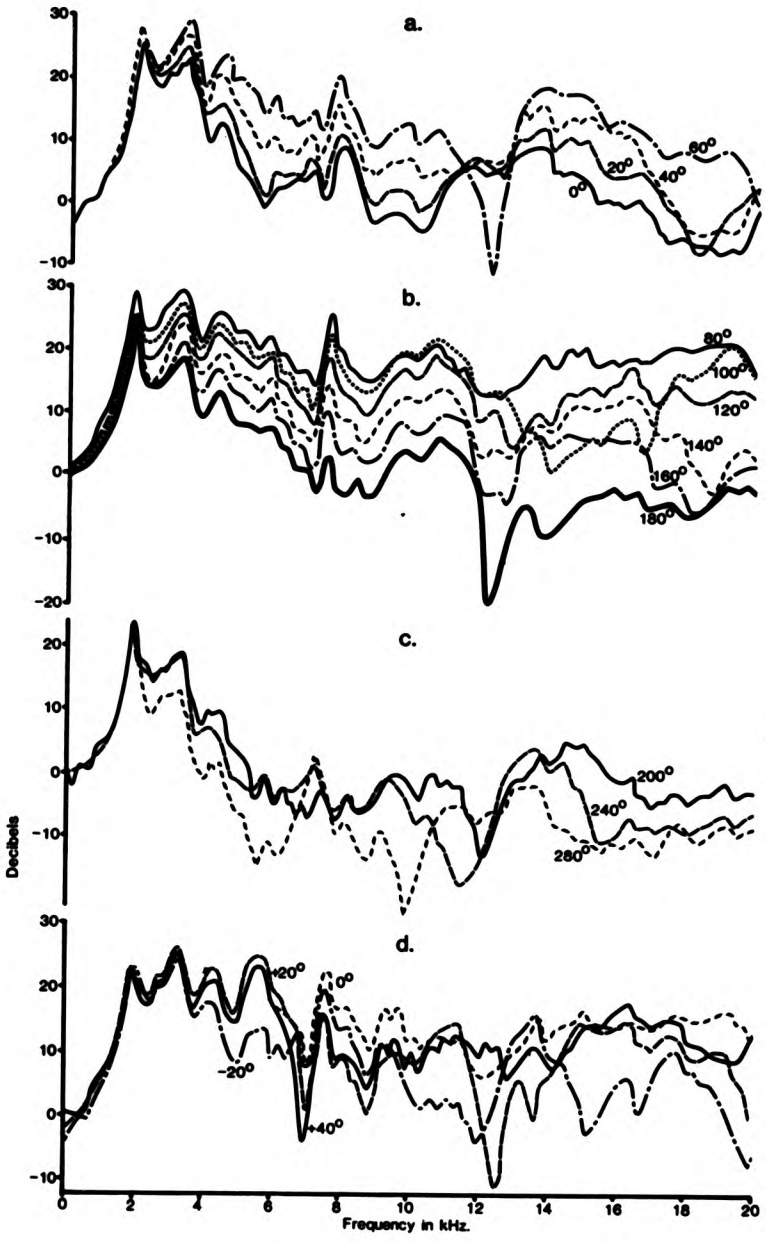

a.
b.
c.
d.
Decibels
Frequency in kHz.
0°
20°
40°
60°
80°
100°
120°
140°
160°
180°
200°
240°
260°
+20°
-20°
+40°

Figure 3.11: Anterior-ipsilateral sector HRTF's from:

(a) the right ear,

(b) the left ear of a cadaver head at 0° elevation. (RP2 right pinna facing 28° azimuth, left pinna facing 12.5° azimuth.)

Fig. 3.11

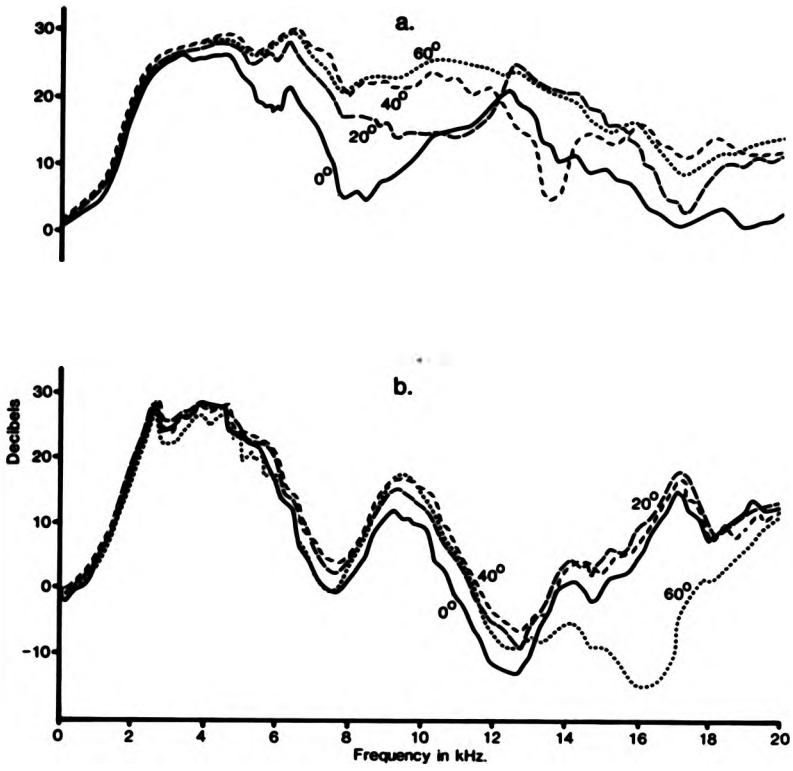

a.
30
20
10
0
60°
40°
20°
0°
b.
Decibels
30
20
10
0
-10
20°
40°
60°
0°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Fig.3.9(d)), they do not show the distinctive changes with elevation that are normally shown by rabbit HRTF's. The HRTF for -40° elevation has been omitted from Fig.3.10(d) for clarity; the function overlapped the -20° elevation HRTF.

Both left and right ears were also studied in animal RP2, a smaller animal with the left pinna measuring 9.3cms in length and the right pinna 9.0cms. Anterior-ipsilateral sector HRTF's for the right and left ears are presented in Fig.3.11(a) and 3.11(b) respectively. The first probe implantation was into the right ear and the family of HRTF's obtained proved relatively normal; a rounded maximum at 2.7kHz was followed by peaks at 4.5kHz and 6.5kHz, null distribution and directional sensitivity being as expected (Fig.3.11(a)). The family of HRTF's obtained subsequently from the left ear, however, showed poor directional sensitivity, apparently associated with losses in gain in the 7.5kHz and 12.5kHz regions, despite the high gain (28dB) at 2.7kHz (Fig.2.11(b)). This reduced directional sensitivity was also found for the left ear HRTF elevation series although the elevation series for the right ear was normal. Deteriorating pinna condition is again a possible cause of the differences between the two ears. In order to examine this possibility more rigorously, an experiment was conducted where HRTF's were collected from a living subject and then during and after the death of that subject. The subject was killed while in the anechoic chamber by a sodium pentobarbitone injection into a vein in the

"unrecorded" pinna. The recorded ear was not moved and the probe remained untouched during this procedure. Fig.3.12 illustrates the changes that occurred. Within 12 minutes of death small losses in gain (up to 2.5dB at 5.5kHz) were already discernible. No further changes occurred over the next 1.5hrs. The preparation was then left in situ overnight; 19hrs after death the HRTF showed an increase of around 8dB in the 3kHz region, 8kHz-11kHz region and 18kHz-20kHz region, but losses of up to 8dB in the 5kHz region. These changes appear to parallel the differences observed between the left and right ears of RP8 and RP4. Increases in HRTF gain may be explained by the stiffening of various parts of the external ear, but the losses are less readily explained. It should, however, be noted that the losses tend to occur at frequencies at which nulls tend to develop. This is discussed further in chapter 4. There were no changes in the frequencies at which HRTF features occurred, indicating that temperature changes in the ear concomitant with death do not have large effects. The right ear of RP9 was also investigated on the day following the death of the animal. The HRTF's obtained from the right ear showed high levels of gain (up to 31dB) in the 3kHz region but did not show unusually low gain in the 5kHz region (Fig.3.13). The similarity between HRTF's obtained from the left and right ears of RP9 is striking, particularly in the shapes and frequency distribution of the peaks.

The most obvious inter-individual variation in HRTF's is

Figure 3.12: HRTF's at 20° azimuth, 0° elevation from RP9 before and after death:

———— alive.

..... 12 minutes after death.

_·_·_·_·_. 19 hours after death. (Left pinna facing 25° azimuth, probe in base of left meatus.)

Figure 3.13: HRTF's at 0° elevation from the right ear of RP9:

(a) anterior-ipsilateral sector,

(b) lateral and posterior-ipsilateral sector.

(Cadaver head, right pinna facing 13° azimuth, probe in base of right meatus.)

Fig. 3.12

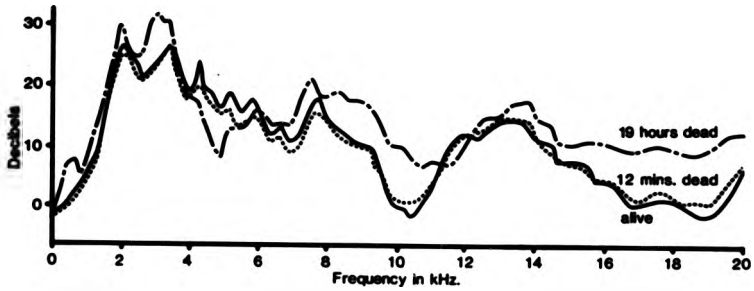


Fig. 3,13

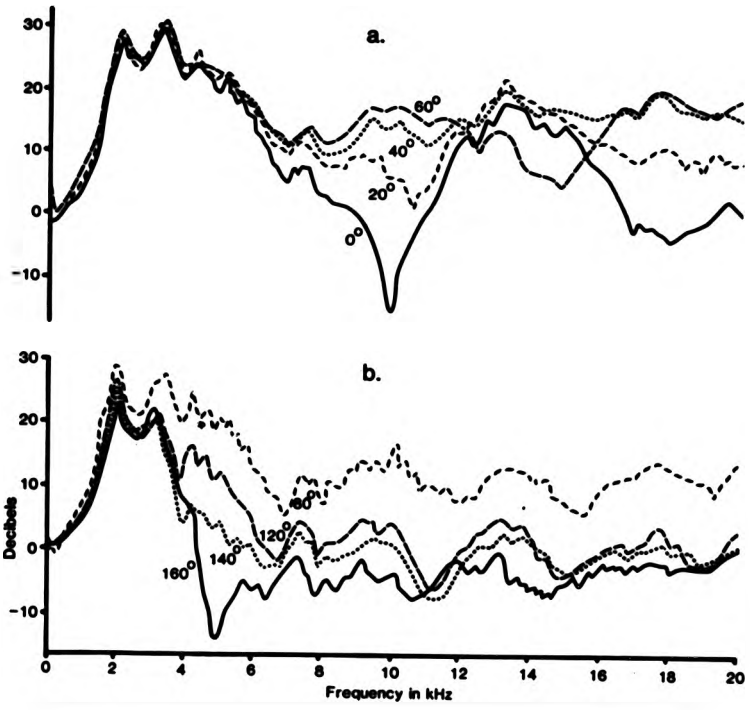


Figure 3.14: HRTF's from a cadaver head
at 0° elevation:
(a) anterior-ipsilateral sector,
(b) lateral and posterior-ipsilateral sector.
(From RP1, right pinna facing 50° azimuth,
probe in base of right meatus.)

Fig. 3.14

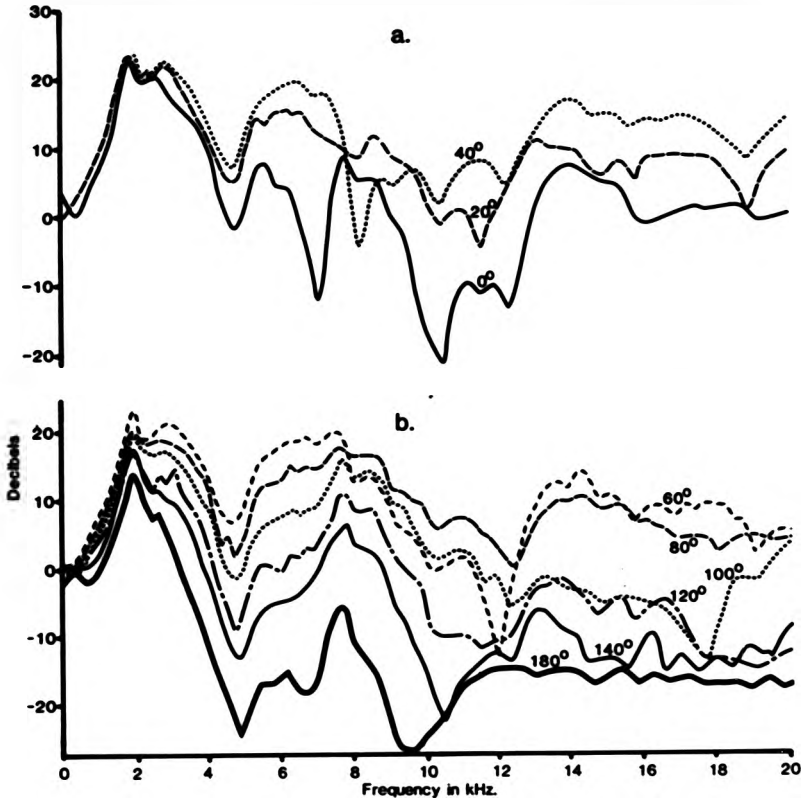
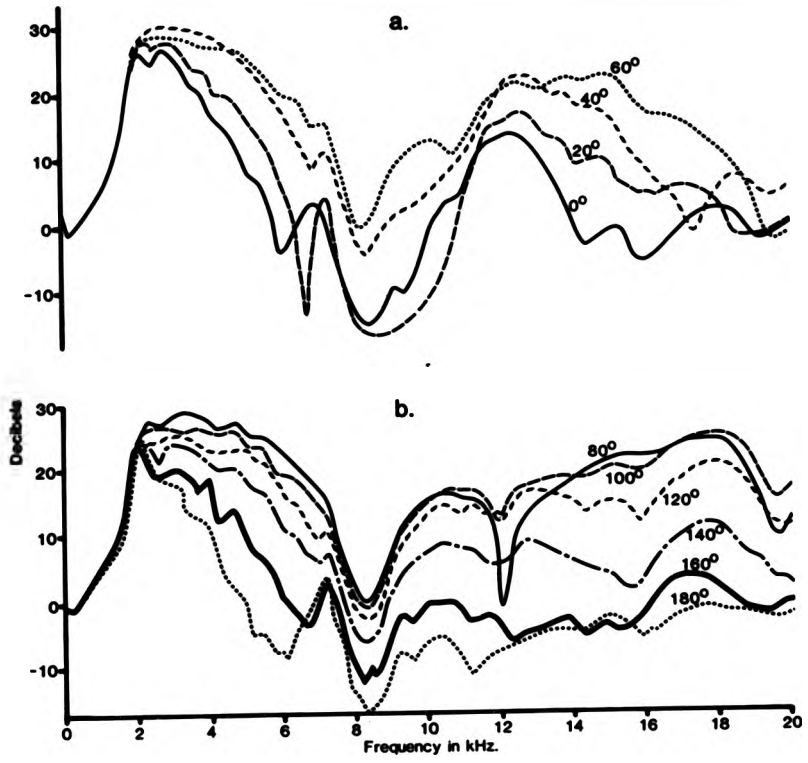


Figure 3.15: HRTF's from a cadaver head
at 0° elevation:
(a)anterior-ipsilateral sector,
(b)lateral and posterior-ipsilateral sector.
(From RP5.left pinna facing 55° azimuth,
probe in base of left meatus.)

Fig. 3.15


a.
30
20
10
0
-10
60°
40°
20°
0°
b.
Decibels
30
20
10
0
-10
80°
100°
120°
140°
160°
180°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

in the number and distribution of peaks. The larger the animal, the lower the frequency at which the first HRTF peak occurs. Thus HRTF's obtained from an unusually large animal, RP1, (its pinnae measured 11.2cm in length) had peaks at 2.0kHz and 3.0kHz (Fig.3.14). This animal also had strong HRTF peaks at 8kHz and high directional sensitivity in the posterior-ipsilateral sector (Fig.3.14(b)). A slightly smaller animal, RP5, with a pinna length of 10.0cm, showed an initial HRTF peak at 2.2kHz, but the next peak was at 2.8kHz (Fig.3.15). This animal also showed unusually high gain in the 2kHz-6kHz region and a consistent peak at 7.3kHz.

3.4. Cochlear Microphonic recordings.

The cochlear microphonic (CM) provides a method of monitoring the effects of the external ear on the sound field which avoids modifying the acoustical properties of the external ear. CM's were obtained from 12 rabbits using the methods described in Chapter 2. CM's of up to 1mV were obtained and in all cases the relationship between signal SPL and CM amplitude was established using both pure tones and broad-band sound. The results for 2 animals are shown in Figs.3.16 and 3.17. The pure tone functions approximate to straight lines over a minimum of 30dB SPL whereas this is the maximum that the broad-band functions could be said to attain. Over this range, the slope of the pure tone functions was 0.98 (R12, Fig.3.16(a)) and 0.93 (R9, Fig.3.17(a)), whereas the broad band functions showed

Figure 3.16: Relationship between CM amplitude and signal SPL at 4 frequencies:
(a) pure tones.
(b) measured from CM spectra obtained using broad-band sound. (From R12, left ear.)
o.....o 2kHz.
Δ_ _ _ _Δ 4kHz.
x_____x 8kHz.
o--------o 16kHz.

Figure 3.17: Relationship between CM amplitude and signal SPL at 3 frequencies:
(a) pure tones.
(b) measured from CM broad-band spectra.(From R9, left ear.)

Fig. 3.16

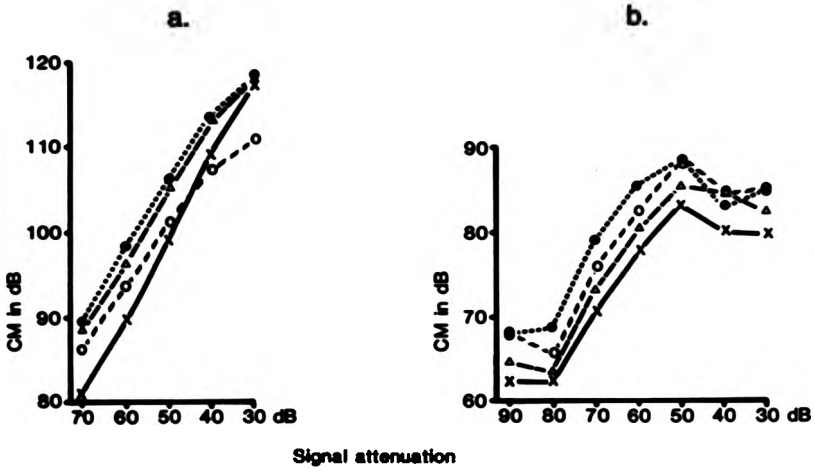
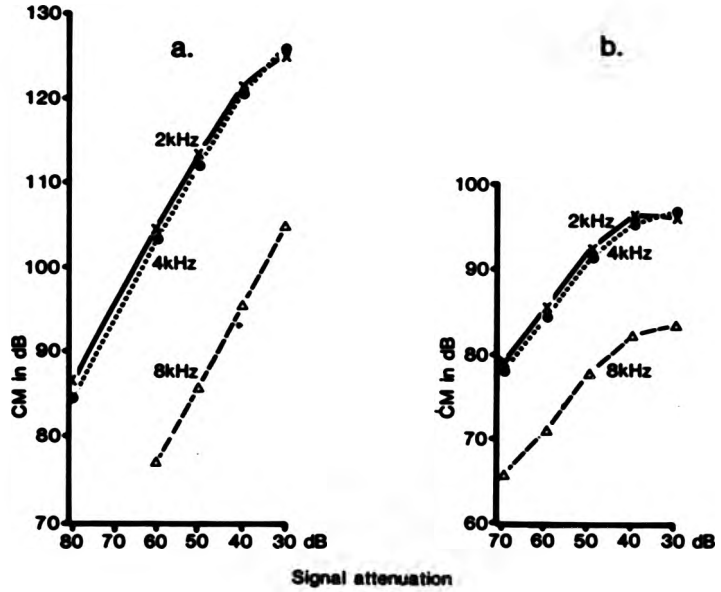


Fig. 3.17



slopes of 0.67 and 0.62 respectively (Fig.3.16(b) and 3.17(b)). Similar differences between the CM responses to pure tones and broad-band sound were found for all 12 rabbits studied in this manner and are a consequence of the CM interference phenomenon. (See e.g. Wever, Bray and Lawrence (1940)). CM interference is probably the result of outer hair cell activity, but elements of two-tone suppression may also be present (Cheatham and Dallos, (1982)). CM spectra from identical sound-source positions were obtained at the start and end of each experiment in order to ascertain the stability of the CM. Only data from stable preparations have been used.

A family of CM spectra at 0° elevation, obtained using broad-band sound, is shown in Fig.3.18. The CM spectra are similar to HRTF spectra (e.g. Fig.3.6) in that peaks and nulls occur in similar frequency regions and similar losses and frequency shifts of nulls occur as the sound source is moved posteriorly (Fig.3.18(c) and contralaterally (Fig.3.18(d)). CM spectra also show characteristic appearances at different elevations of the sound-source (Fig.3.19) which are associated with the levels of gain and the development of nulls in the 1kHz-8KHz region. The spectrum for 0° elevation, 40° azimuth, (Fig.3.19(a)) has been omitted for clarity and because a distinct null was absent. Fig.3.19(b) shows a similar spectrum.

The most directionally sensitive set of CM spectra were obtained from R9 (rabbit number 9 in the CM series). These

Figure 3.18: CM spectra from :

(a) anterior-ipsilateral,

(b) lateral-ipsilateral,

(c) posterior-ipsilateral,

(d) contralateral sectors at 0° elevation.

(From R12, left pinna facing 13° azimuth)

Fig. 3.18

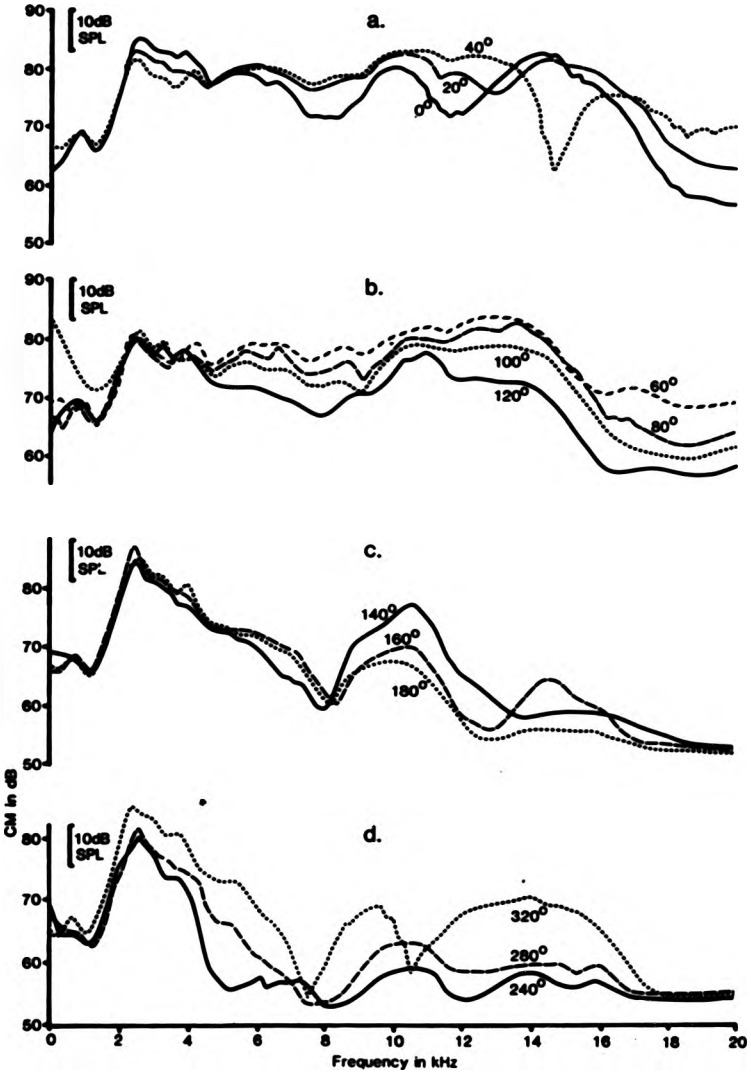

a.
b.
c.
d.
10dB SPL
40°
20°
0°
100°
120°
60°
80°
140°
160°
180°
320°
280°
240°
CM in dB
Frequency in kHz

Figure 3.19: CM spectra at various elevations at:

(a) 40° azimuth,

(b) 80° azimuth. (From R12, left pinna facing 13° azimuth.)

Fig. 3.19

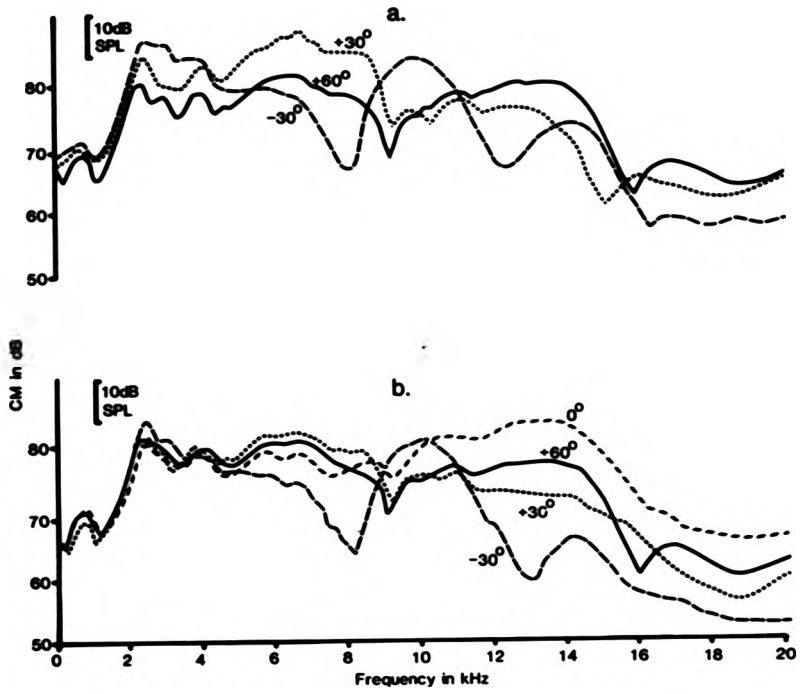

a.
10dB
SPL
+30°
+60°
-30°
80
70
60
50
CM in dB
b.
10dB
SPL
0°
+60°
+30°
-30°
80
70
60
50
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz

Figure 3.20: CM spectra at 0° elevation:
(a) anterior-ipsilateral.
(b) lateral and posterior-ipsilateral.
(c) contralateral sectors. (From R9, left pinna facing 40° azimuth.)

Fig. 3.20

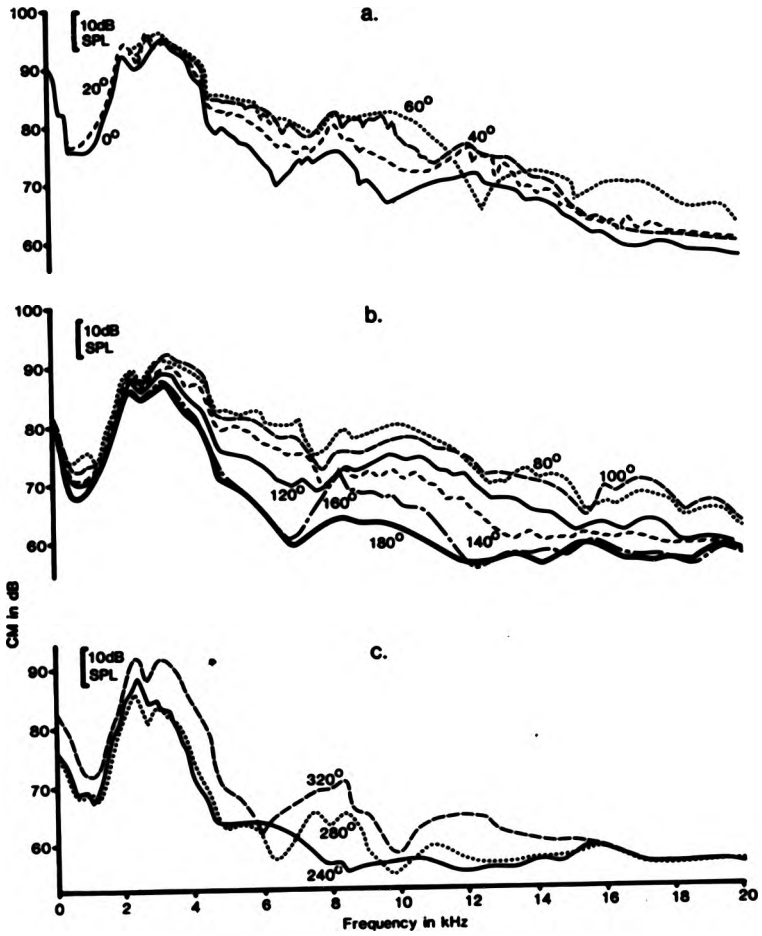
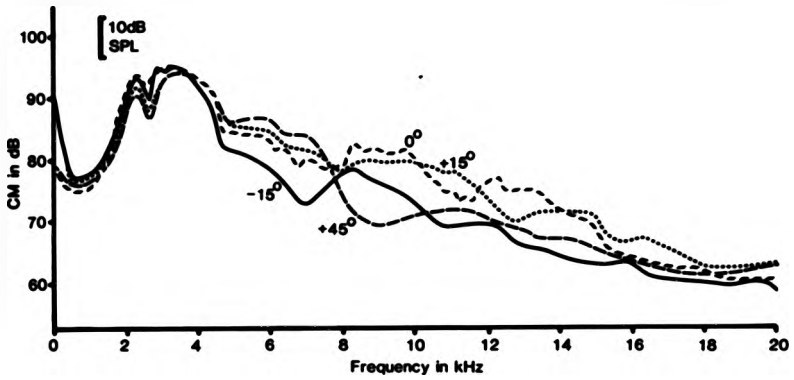

a.
b.
c.
10dB SPL
0°
20°
40°
60°
80°
100°
120°
140°
160°
180°
240°
260°
320°
CM in dB
Frequency in kHz

Figure 3.21: CM spectra at various elevations at 40° azimuth. (From R9, left pinna facing 40° azimuth.)

Fig. 3.21


10dB
SPL
100
90
80
70
60
CM in dB
0°
+15°
-15°
+45°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz

are shown in Fig.3.20. These spectra show peaks at 2.3kHz, 3.3kHz and 8.3kHz which is typical of the HRTF peak distribution found in the RP series. Some degree of sensitivity to the elevation of the sound-source was also found in R9: spectra at 4 angles of elevation at 40° azimuth are shown in Fig.3.21.

In general, CM spectra obtained from rabbits other than R9 did not show R9's level of directional sensitivity. High levels of CM interference are probably responsible for this. The CM's obtained from R9 were of exceptionally high voltage which enabled lower signal SPL's to be used. This in turn reduced the levels of CM interference, giving greater dynamic range and spectral feature clarity.

3.5. Interaural Intensity Differences (IID's)

The directional sensitivity of the ear can also be represented in terms of IID's. The assumptions underlying the calculation of IID's is that the sound is received by both ears (not always the case) and that both ears effect identical SPL transformations. For an animal with mobile pinnae, it must also be assumed that the pinnae are symmetrically positioned.

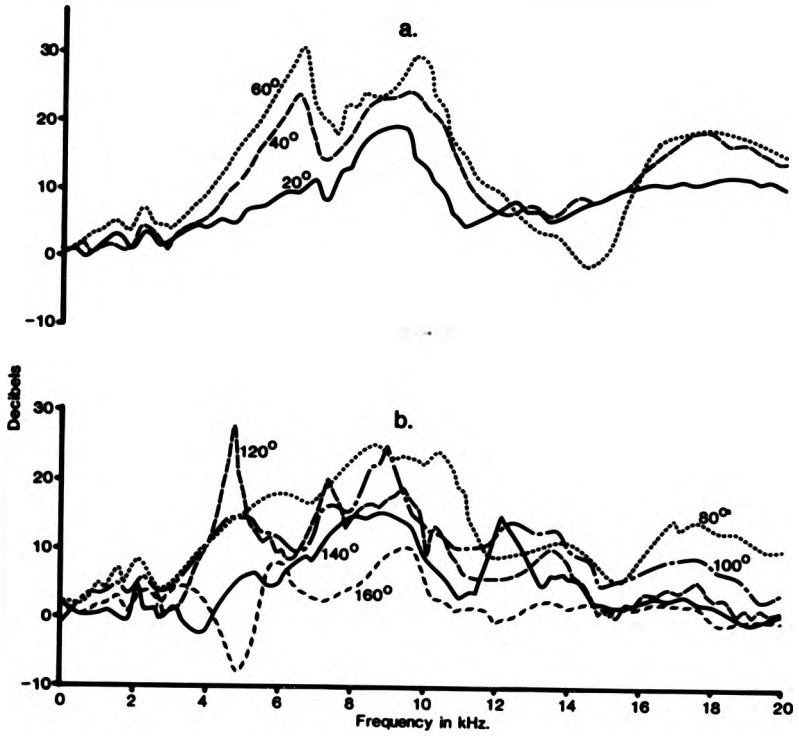
It is possible to represent IID's at single frequencies as azimuthal (or elevational) dependence functions. Alternatively, IID frequency/intensity spectra for one particular position of the sound-source can be used. For an insect approaching a potential mate using phonotaxis, azimuthal dependence functions are probably the more

Figure 3.22: IID spectra from a cadaver head at 0° elevation:

(a) anterior.

(b) lateral-posterior sector. (From RP9, right pinna facing 32° azimuth, probe in base of right meatus.)

Fig. 3.22


a.
60°
40°
20°
30
20
10
0
-10
b.
120°
140°
160°
80°
100°
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

appropriate because the signal is of sufficient duration to allow scanning and triangulation and very often particular "carrier" frequencies are being responded to. For mammals such as the rabbit, however, broad-band sounds of brief duration (e.g. from a stalking predator) often have to be localised; IID spectral representation is more appropriate for this.

A series of IID spectra at 0° elevation is presented in Fig. 3.22. The anterior quadrant spectra (Fig.3.22(a)), show two sharp peaks at about 6.5kHz and 9.5kHz and broader covert maxima in the 16kHz-18kHz region. There is an orderly progression of IID values with angle of azimuth from 20° to 60° but thereafter (Fig.3.22(b)) the IID spectra overlap, peaks occurring at different frequencies for different angles of azimuth. The peaks in the IID spectra are caused by nulls in the contralateral HRTF's and it is the frequency shifting of the posterior sector contralateral nulls that causes the IID's from the posterior sector to overlap. In some preparations, orderly progressions of IID spectra occurred in both anterior and posterior sectors. An example of this is shown in Fig.3.23. IID spectra obtained at different elevations tend to have a characteristic appearance conferred by the distribution of peaks and troughs. Fig.3.24 shows a series of spectra obtained at -30° and +30° elevation (compare the 0° elevation series for this animal in Fig.3.23). The anterior sector spectral features show an upfrequency shift of 2kHz or more over 60° of elevation; the first peak occurs at

Figure 3.23: IID spectra obtained from a cadaver head at 0° elevation;
(a) anterior,
(b) posterior sector. (From MG16, right pinna facing 34° azimuth, 1/4inch microphone in right tympanic bulla.)

Fig. 3.23

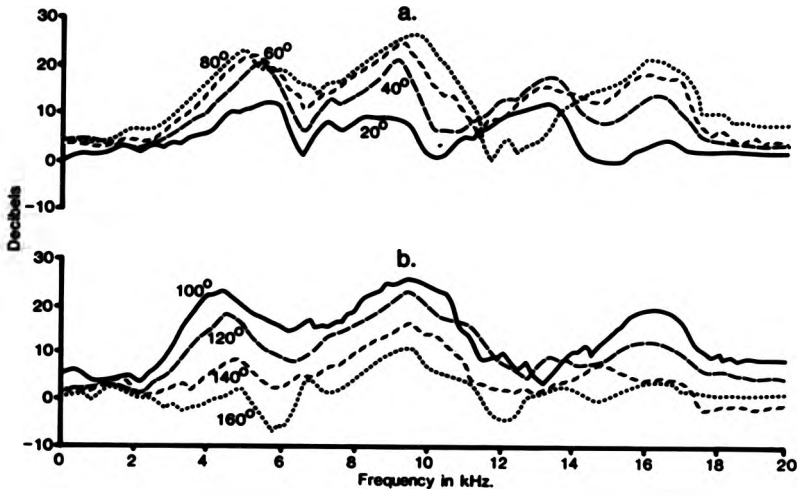
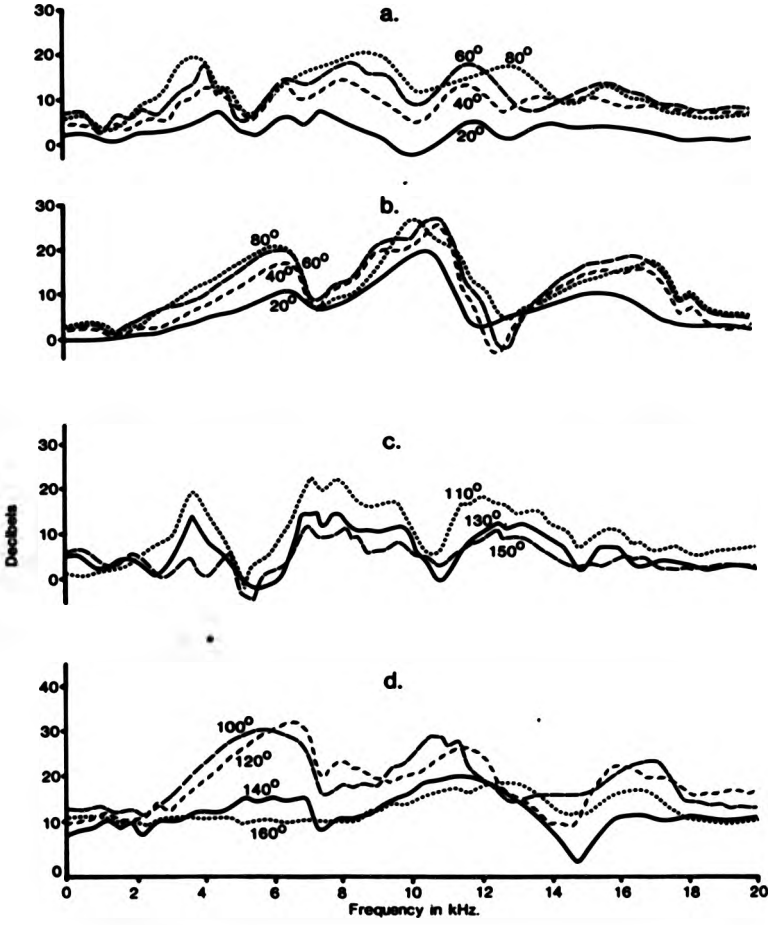

a.
b.
80°
60°
40°
20°
100°
120°
140°
160°
Decibels
30
20
10
0
-10
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 3.24: IID spectra obtained from a cadaver head.
(a) anterior sector at -30° elevation.
(b) anterior sector at +30° elevation.
(c) posterior sector at -30° elevation.
(d) posterior sector at +30° elevation.
(From MG16, right pinna facing 34° azimuth, 1/4inch microphone in right tympanic bulla.)

Fig. 3.24


a.
60°
80°
40°
20°
b.
80°
40°
60°
20°
c.
110°
130°
150°
d.
100°
120°
140°
160°
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

about 4kHz at -30° elevation (Fig.3.24(a)) and at about 6.5kHz at +30° elevation (Fig.3.24(b)); the first null and second peak show similar up-frequency shifts. This pattern is repeated in the posterior sector spectra (Fig.3.24(c) and (d)).

IID spectra were also obtained during the experiments where the CM was being monitored. Unlike the monaural spectra, CM IID spectra are directly comparable with IID SPL spectra and, indeed, are often indistinguishable from them. A series of CM IID spectra is shown in Fig.3.25. The anterior quadrant spectra show excellent directional sensitivity and spectra for every 10° azimuth over the anterior quadrant have therefore been figured (Fig.3.25(a) and (b)). Best separation of IID spectra is shown between 0° and 40° azimuth which is a typical result for a preparation with forward facing pinnae (13° azimuth in this case). Characteristic changes in CM IID spectra also occurred with increasing elevation of the sound source (Fig. 3.26). The greatest amount of up-frequency movement of spectral features occurs between -30° and 0° elevation but +30° elevation shows distinct differences from +60° elevation at higher frequencies, notably the very high frequency of the major peak in the +60° elevation spectrum (13kHz in Fig.3.26(b) and 15kHz in Fig.3.26(a)).

A less directionally sensitive series of CM IID spectra from R9 is shown in Fig.3.27. The spectral features are shifted down-frequency as compared with R12 (Fig.3.25). A likely cause of this is the slightly larger pinnae of R9

Figure 3.25: CM IID spectra at 0° elevation:

(a) anterior.

(b) antero-lateral.

(c) lateral.

(d) posterior sectors. (From R12, left pinna facing 13° azimuth.)

Fig. 3.25

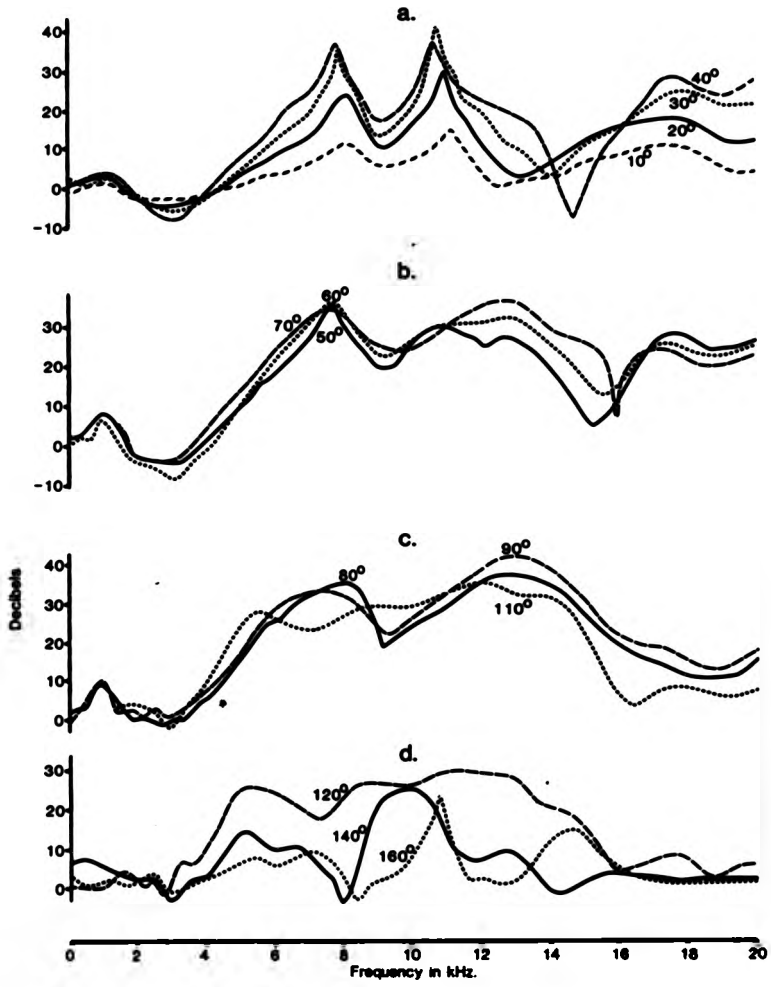

a.
40
30
20
10
0
-10
40°
30°
20°
10°
b.
30
20
10
0
-10
70°
60°
50°
c.
Decibels
40
30
20
10
0
80°
90°
110°
d.
30
20
10
0
120°
140°
160°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 3.26: CM IID spectra for various elevations at:

(a) 40° azimuth,

(b) 80° azimuth. (From R12, left pinna facing 13° azimuth.)

Fig. 3.26

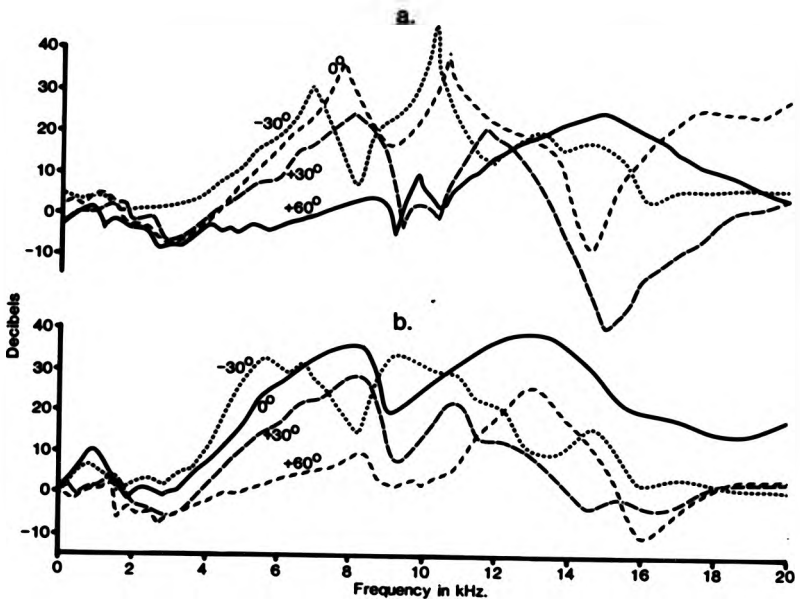

a.
b.
-30°
0°
+30°
+60°
Decibels
40
30
20
10
0
-10
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 3.27: CM IID spectra at 0° elevation:
(a) anterior sector.
(b) posterior sector. (From R9, left pinna facing 40° azimuth.)

Figure 3.28: CM IID spectra for 3 elevations at 80° azimuth. (From R9, left pinna facing 40° azimuth.)

Fig. 3.27

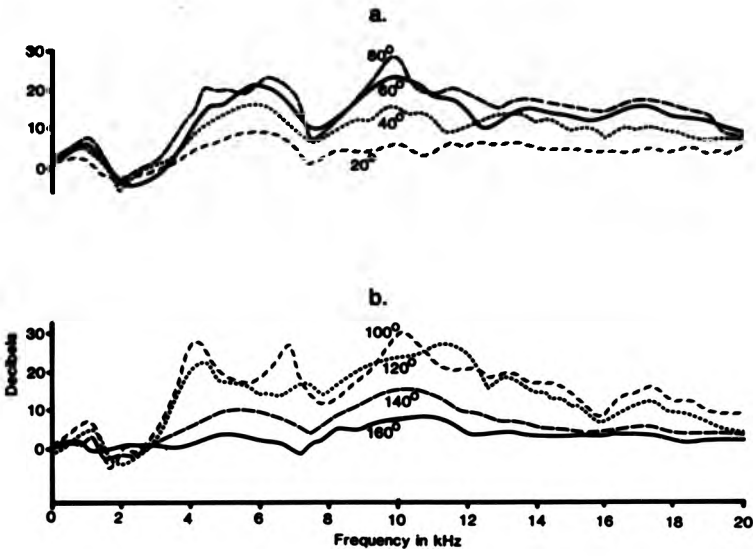
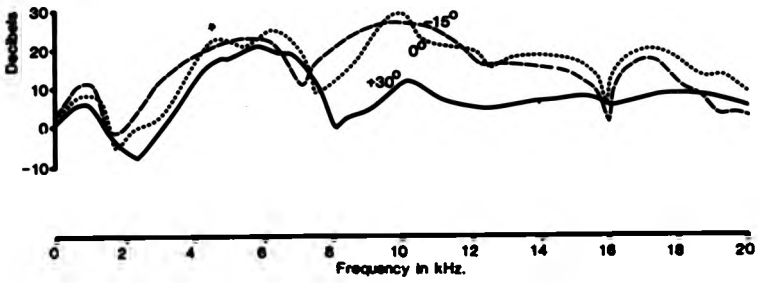


Fig. 3.28



but an additional cause may have been the more ventral orientation of the pinnae. Accurate control of the vertical orientation of the pinnae during experiments was difficult; small inaccuracies could result in frequency shifts in spectral features because of the sensitivity of the spectral features to elevation. An IID elevation series for R9 is shown in Fig.3.28; there is approximately a 300Hz-400Hz up-frequency shift of the 0° nulls as compared with the -15° spectrum nulls, whereas this increases to about 600Hz between +30° and 0°. In R12 (Fig.3.26) the situation appears to be reversed, there being only a 300Hz shift between +30° and 0°. This indicates a more ventral orientation of the pinna in R9.

In general, IID spectra obtained from the CM resemble SPL IID spectra, showing similar levels of directional sensitivity (in the most sensitive CM preparations) and similar distributions and frequency shifts of spectral features. The non-monotonic nature of IID spectra is clear from these studies and to what extent the animal can make use of actual IID values is questionable. In order to illustrate this point CM IID's obtained from R12 have been plotted as functions of angle of azimuth at 6kHz, 7kHz and 8kHz (Fig.3.29). Reference to Fig.3.25 will show that these 3 frequencies are in the vicinity of a sharp peak in the IID spectrum; the closer to the peak, the larger the IID. Thus the function for 8kHz in Fig.3.29 shows a greater gradient in the anterior sector (where the IID peak is more prominent) than the function for 7kHz, which in turn shows

Figure 3.29: CM IID'S plotted as functions of azimuth at 0° elevation at:

x_____x 6kHz,

o.....o 7kHz,

Δ-----Δ 8kHz. (From R12, left pinna facing 13° azimuth.

Figure 3.30: IID's plotted as functions of azimuth at 0° elevation at:

o_____o 4kHz,

x-----x 8kHz,

o.....o 16kHz. (From MG16, right pinna facing 34°, 1/4inch microphone in right bulla.)

Figure 3.31: IID's plotted as functions of angle of azimuth at 0° elevation at 7kHz with the pinna facing 45° azimuth x_____x, and o----------o 70° azimuth. (From MG14, 1/4inch microphone in left bulla.)

Fig. 3.29

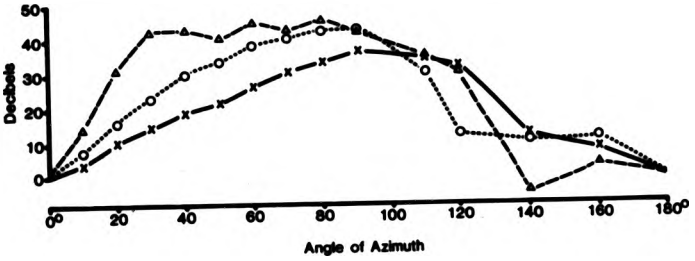


Fig. 3.30

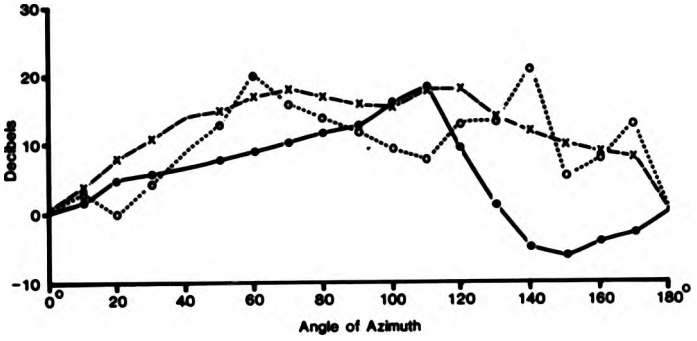
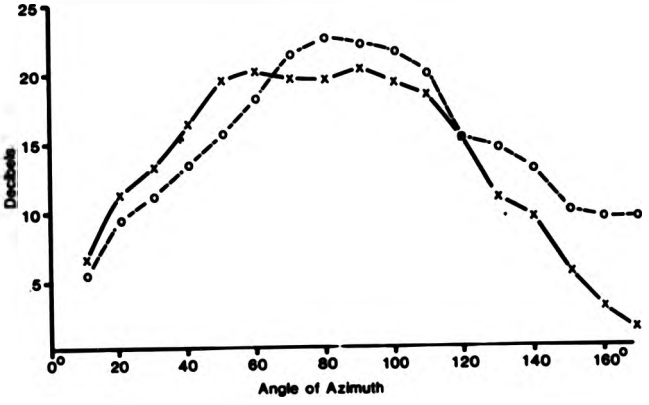


Fig. 3.31



a greater gradient than the function for 6kHz. In other words, IID values are dependent on frequency. That this dependence is non-monotonic can be seen from any of the IID spectrum series shown above. Fig.3.30 shows SPL IID's as functions of angle of azimuth at 3 frequencies at octave intervals; the differences between frequencies are again clear.

The most directionally sensitive parts of the IID spectrum occur at, or near, IID spectrum peaks. The main cause of these peaks is contralateral nulls. The value or depth of the nulls depends on the ratio of signal amplitude to background noise level. IID's are therefore likely to vary to some extent with signal amplitude. However, for a moving sound source, or when the pinnae are moved, changing IID values are likely to be of more use than monaural SPL's because of the strong directional sensitivity conferred by the contralateral nulls. The direction in which the pinnae are facing affects the strength of this cue; IID functions rise more uniformly and often more sharply in the sector faced by the pinnae. This point is illustrated in Fig.3.31, where IID functions at 7.0kHz for 2 different pinna positions are shown. The IID function shows a greater gradient in the anterior sector when the pinna is facing 45° azimuth, but gives better directionality at the more lateral angles when the pinna is facing 70° azimuth.

CHAPTER 4. RESULTS: FURTHER EXPERIMENTS ON THE RABBIT.

4.1. Introduction.

The HRTF of the rabbit can be expected to be the result of the interactions of gains from a number of different sources: standing wave resonances and their harmonics are likely to be associated with the ear canal and perhaps the pinna cavities; diffraction and reflection from the pinna surface; and gain resulting from the mouth : throat ratio of the external ear.

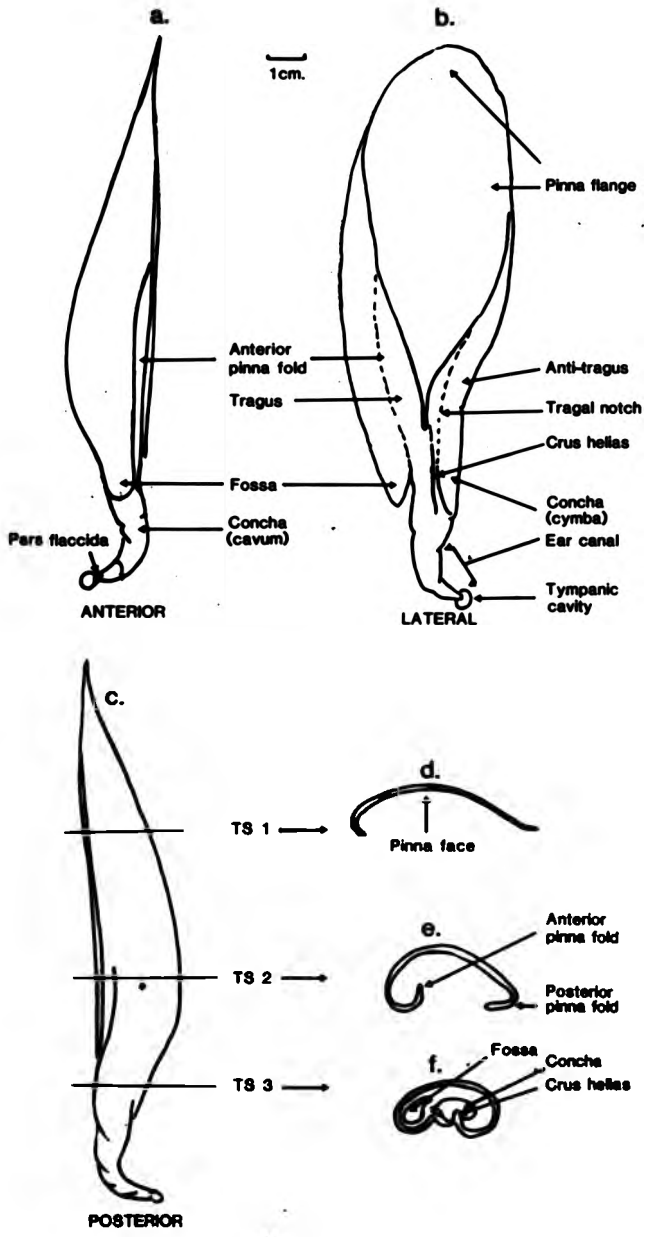
The cavity system of the external ear is, of course, open to the sound field, and presumably acoustically coupled throughout. It is not practicable, therefore, to attempt to isolate the different sources of gain by locating a probe in different parts of the system. Interference with the system by, for example, cutting parts of it away or blocking-off parts of it must therefore be resorted to. Unfortunately, because the system is acoustically coupled, interference with one element is likely to affect other elements, making interpretation of the results of such interference difficult. Because of this, a number of different experimental approaches have been used to investigate the acoustical properties of the various subdivisions of the external ear.

4.2. Anatomy of the External Ear.

Endocasts of the external ears of experimental subjects were made using casting plaster or silicon moulding rubber

Figure 4.1: Drawings of the right external ear of a New Zealand White rabbit: (a), (b) and (c) are anterior, lateral, and posterior views respectively of a composite based on endocasts and external views; (d), (e) and (f) are cross-sections of the pinna taken at the levels indicated in 4.1(c).

Fig. 4.1


a.
b.
1cm.
Pinna flange
Anterior pinna fold
Tragus
Fossa
Concha (cavum)
Pars flaccida
ANTERIOR
Anti-tragus
Tragal notch
Crus helias
Concha (cymba)
Ear canal
Tympanic cavity
LATERAL
C.
TS 1
TS 2
TS 3
POSTERIOR
d.
Pinna face
e.
Anterior pinna fold
Posterior pinna fold
f.
Fossa
Concha
Crus helias

(Silastic E). Obtaining a complete fill of the external ear proved difficult because air tended to be trapped in the base of the meatus. Satisfactory fills were eventually obtained by boring a small hole in the meatus wall opposite the TM and filling with Silastic E under vacuum (760mm Hg) for 2-3hrs. Fig.4.1 shows drawings of the external ear of RP8 from 3 different angles. In each case the drawing is a composite of both endocast and an external view of the pinna. The pinna opening is flanked by two folds, the anterior and posterior pinna folds, which are associated with the "fossa" and "cymba" respectively (see Fig.4.1(e) and (f)). The "fossa" is a pocket about 6mm deep, whereas the "cymba" is a part of the concha demarcated by a strong ridge, the "crus helias". The concha narrows gradually from an average radius of about 6mms at the level of the fossa to 4mm at the entrance to the meatus. There is no clear demarcation between concha and ear canal. The ear canal bends through almost 90° and narrows gradually to 2mm radius at which point it enters a disc-shaped cavity of 3mm radius and maximum depth of 1.5mm. This cavity is situated within the tympanic bulla and lies lateral to the TM which forms its medial wall. The impression left by the pars flaccida is depicted in Fig 4.1(a).

4.3. Pinna Removal.

Removal of the pinna, either in stages or in its entirety, was carried out on 11 occasions. Removal of the whole of the pinna left the cut distal end of the meatus

Figure 4.2: HRTF's obtained at 0° elevation:

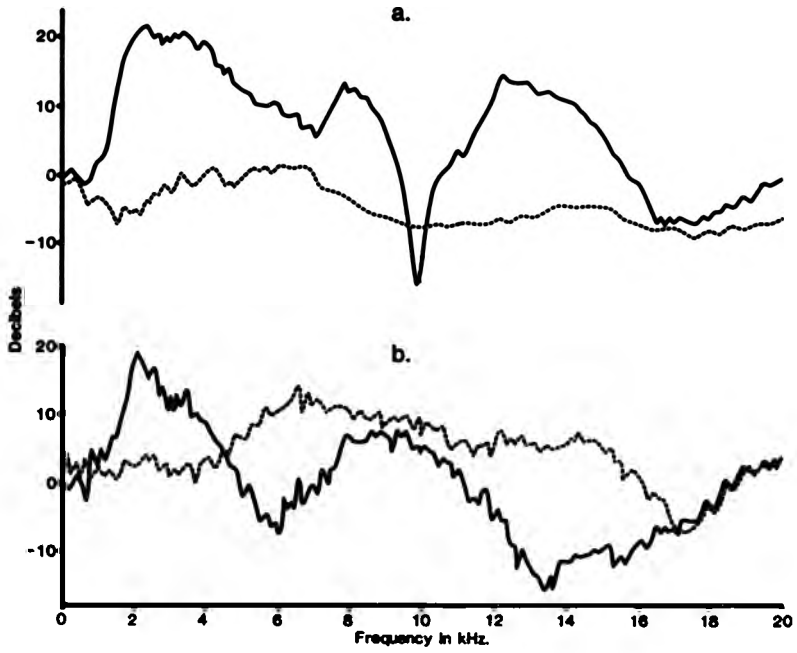
(a) at 0° azimuth,

(b) at 140° azimuth,

_____ pinna intact,

..... pinna removed. (From RP10, cadaver, left pinna facing 18° azimuth).

Fig. 4.2



flush with a shallow bowl gouged out of the muscle surrounding the pinna-base. Free-field : TM transfer functions obtained in these circumstances vary considerably. In experiments where a microphone had been implanted directly into the base of the meatus, gain of up to 18dB centred at 5kHz-6kHz was recorded. However, when probes inserted into the tympanic cavity were used, gain in the transfer function was generally below 10dB (Fig.4.2). Removing the pinna changes the orientation of the ear opening from anterior to dorsal/posterior. Fig.4.2 therefore shows transfer functions at an anterior (Fig.4.2(a)) and posterior (Fig.4.2(b)) angle of azimuth. It can be seen that the pinna-removed functions show more gain at 140° azimuth than at 0° azimuth whereas the converse is true for the pinna-present functions. Maximum gain occurs at different frequencies for the pinna-removed functions, depending on the angle of incidence of the sound. The length of ear canal remaining, as determined from a Silastic E endocast, was 2.0cm, and the mean diameter of the cut end was 7mm. The fundamental axial resonance of the canal should occur at:

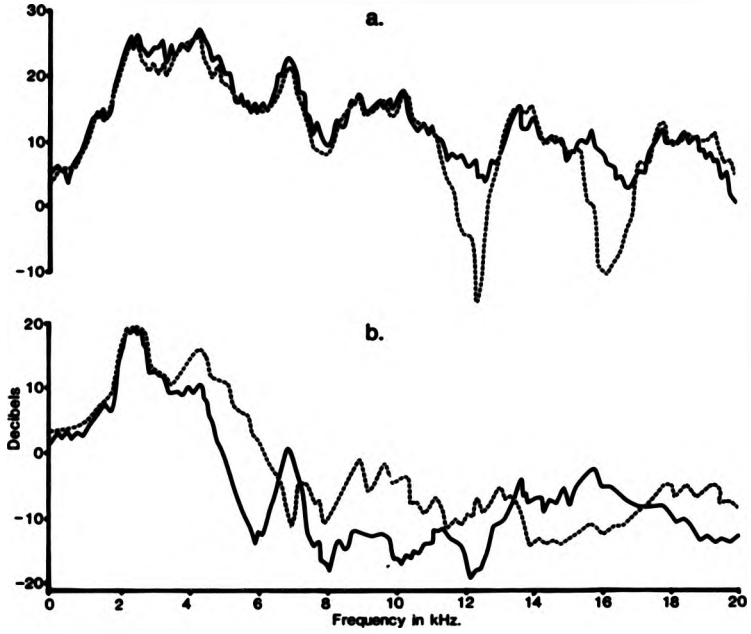
$$1/4(C/(L+0.6A)$$

where C is the speed of sound (taken to be 344m/sec), L is the length of the canal (0.020m) and A is the radius of the canal (0.0035m max), (see Beranek (1954)). This gives a value of 3.891kHz which is too low to account for any of the regions of major gain in the pinna-removed transfer functions. The broad-based gain in the latter functions is

Figure 4.3: HRTF's obtained at 0° elevation:
(a) at 0° azimuth.
(b) at 280° azimuth.
_____ pinna intact.
..... top 5cm of pinna removed. (From RP8 cadaver head, under meatus blocked conditions, right pinna facing 70° azimuth.)

Figure 4.4: HRTF's obtained at 28° azimuth, 0° elevation with various amounts of pinna removed:
(a) _____ 4cm, ... 6cm and ------- 9.3cm removed:
(b) ..... 9.8cm and _____ 10.7cm removed. (From RP2, cadaver head, right pinna facing 28° azimuth.)

Fig. 4.3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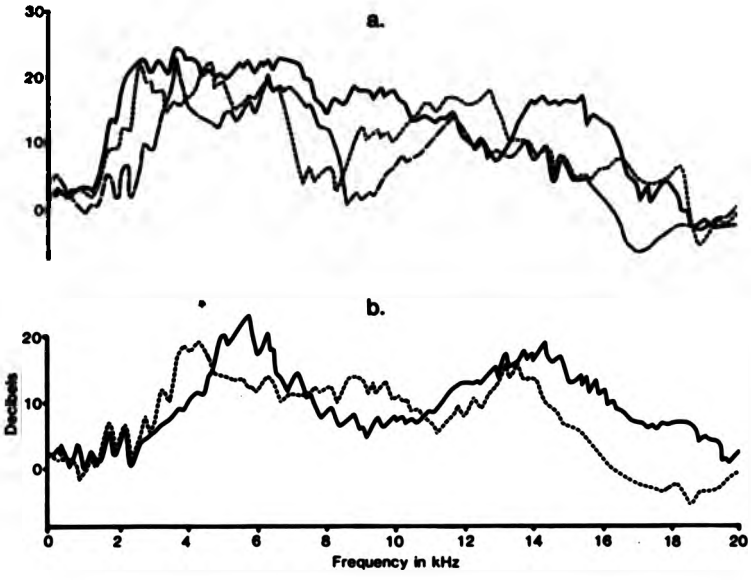
Frequency in kHz.

Fig. 4.4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Frequency in kHz

reminiscent of diffraction of sound at normal incidence to a body such as a cylinder (Olson (1957)). Gain would be maximal for sound of wavelength equal to the diameter of the cylinder. The wavelength of sound at 6kHz is 5.7cm which is close to the mean posterior view diameter (5.75cm) of the head of the rabbit (RP10) from which the data in Fig.4.2 were obtained.

Six experiments were carried out where the pinna was removed in sections. Fig.4.3 shows that when the top 5cm of the pinna is removed there is slight loss of gain at most frequencies above 2.5kHz when the sound is on axis to the sound source (Fig.4.3(a)). The deeper nulls at 12.5kHz and 16kHz are interesting, but the causes of nulls are complex and this finding is not easily interpreted (see below). When the sound is off-axis to the ear (Fig.4.3(b)), cutting down the pinna results in increased gain at most frequencies above 3.5kHz. This increase is 10dB or more over much of the 4kHz-13kHz range and is presumably due to the loss of pinna shadowing (reflection and diffraction) effects. The major effect of the top part of the pinna, therefore, is to reduce off-axis high frequency gain; this part of the pinna is, therefore, a major contributor to the directionality of the external ear.

Removal of more of the pinna results in greater on-axis loss and up-frequency shifts of a number of features in the transfer function. Fig.4.4 shows a series of transfer functions obtained from a probe implant into the tympanic cavity of a cadaver head. The sound source was kept on-axis

to the ear as 4cm, 6cm, and then 9.3cm of pinna were removed (Fig.4.4(a)). The loss of gain and up-frequency shift of the low-frequency peak are clear. These trends continue in Fig.4.4(b) where functions obtained after 9.8cm and 10.7cm of pinna had been removed are shown. Since the shortening of the concha is accompanied by the up-frequency shift of a distinct peak (initially at about 2.7kHz in this specimen), it may be that the peak is the result of an axial resonance associated with the concha. Ignoring end corrections for the moment, this would imply that the functional depth of the concha is about 3.2cm or less. This is the approximate distance between the top of the tragal notch and the entrance to the meatus.

4.4. Blocking the Meatus.

Six sets of observations were made on rabbits where the entrance to the ear canal was blocked by a tight fitting plug of plasticene. The probe was situated in the centre of the plug with the probe opening flush with the plug surface. This was achieved by threading the probe through a small hole in the meatus wall and thence up the meatus and through the plug. Where possible, the shape of the plug had been determined by reference to an endocast of the other external ear of that animal. A typical result is shown in Fig.4.5; the blocking results in loss of gain up to about 7.5kHz but at some higher frequencies there is a slight increase in gain (disregarding the loss of the null at 11.5kHz). Despite the changes in gain, however, the major

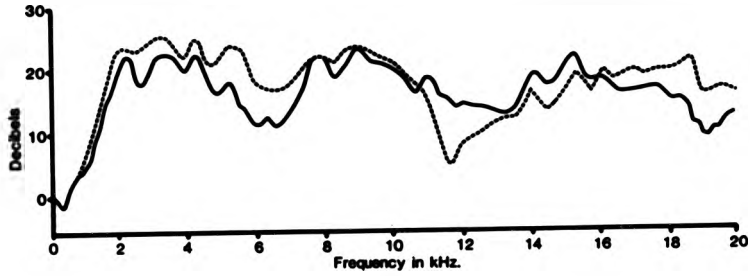
Figure 4.5: HRTF's obtained at 80° azimuth. 0° elevation with:

..... probe in the base of the meatus

_____ probe in a plug in the base of the concha. (From RP8, cadaver head, left pinna facing 80° azimuth.)

Figure 4.6: HRTF obtained at 180° azimuth. 0° elevation with 1.8cm of concha remaining. Probe in plug at base of meatus. (From RP9 cadaver head).

Fig. 4.5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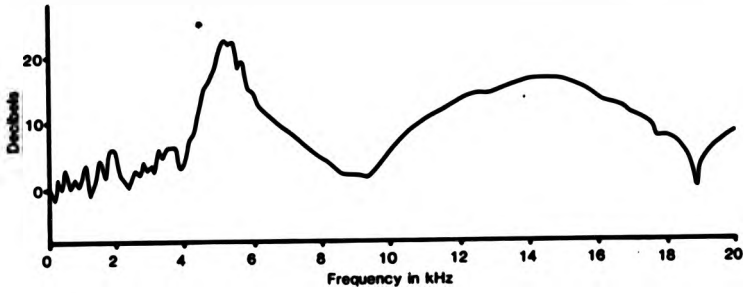
Frequency in kHz.

Fig. 4.6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Frequency in kHz

features of the HRTF are retained in the meatus blocked function, and there is no obvious region in the latter function which could be said to suffer from loss of a meatus-based standing wave resonance. The general loss in gain up to 7.5kHz may, in part, be explained by loss of the transformation (as in a conical horn, for example) from the broad base of the concha to the narrow end of the meatus. The increased gain at some of the higher frequency regions may be associated with increased reflection from the plug. The slight up-frequency shift in the low frequency peak from 2.0kHz to 2.2kHz is probably because of the slight protrusion of the plug into the effective concha volume.

Pinna removal was carried out on 2 occasions under meatus blocked conditions. The reason for this was that HRTF features tend to be "sharpened" by meatus-blocking, as can be seen in Fig.4.5, and following the up-frequency movement of spectrum features was consequently made easier. The final transfer function obtained from one such experiment is shown in Fig.4.6; a peak of 23dB at 5.2kHz is followed by a broader region of gain centered at 15kHz. The concha had been reduced to a bowl shaped depression 1.8cm deep with the probe sited in the plasticene plug in its base. The obvious interpretation of this transfer function is that an axial resonance of the concha bowl is the source of the 5.2kHz peak (1/4 wavelength = 1.65cm) and that the peak in the 15kHz region is the first harmonic. This transfer function is similar to transfer functions obtained under

pinna-cut, meatus-open conditions, (e.g. the 10.7cm removed function in Fig.4.4(b)), and therefore a strong resonance associated with the meatus appears to be ruled out.

4.5. Alteration of the Acoustic Impedance of the TM.

The apparent lack of a standing wave resonance associated with the ear canal of the rabbit could, in part, be associated with a naturally low acoustic impedance of the TM. Several experiments were therefore carried out where modifications to TM impedance were attempted.

(a)Insertion of a microphone membrane in place of the TM. Insertion of a 1/8 inch microphone into the base of the meatus after removal of the TM resulted in HRTF's of unusually high gain (up to 38dB) in the 2kHz-4kHz range and also at higher frequencies which approximated to harmonics of the low frequency gain. Insertion of the microphone appeared to promote standing wave resonances associated presumably with the meatus. Fig.4.7 shows sample HRTF's from one such experiment where increases of 8dB or more in the 3kHz-4kHz range and increases of up to 15dB in the 11kHz-13kHz range accompany microphone insertion.

(b)Filling the tympanic bulla by syringing water in through a hole in the bulla wall was attempted on 2 occasions but subsequent post-mortems revealed that the tympanic membrane had ruptured on both occasions. This experiment was therefore abandoned.

(c)Coating the TM with cyanoacrylic cement was carried

Figure 4.7: HRTF's obtained at 0° azimuth, 0° elevation:

———— probe in base of meatus (RP9, alive),

..... 1/8 inch microphone in base of meatus, (RP9, cadaver head).

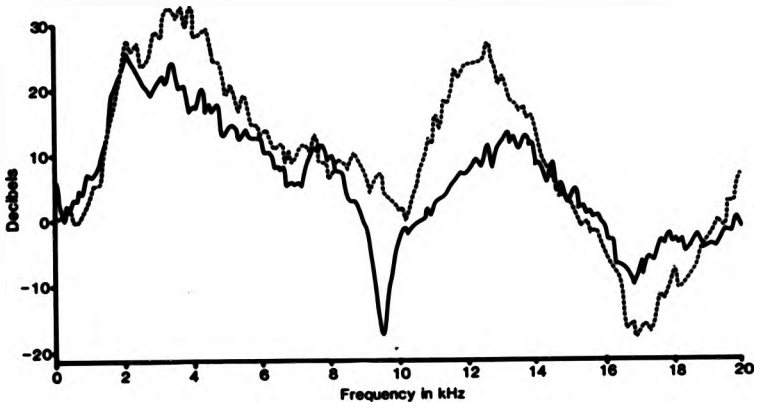
Figure 4.8: HRTF's obtained "on-axis" with:

..... TM punctured (probe in meatus),

———— TM coated with cyanoacrylic cement (probe in meatus),

---------- probe in plug in base of concha. (From RP7, cadaver head.)

Fig. 4.7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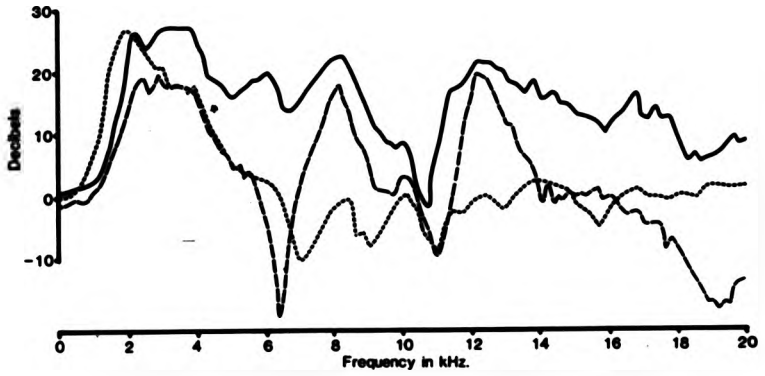
Frequency in kHz

Fig. 4.8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Frequency in kHz.

out twice via a large hole cut in the wall of the tympanic bulla. Cyanoacrylic cement sets hard and the coated TM's were therefore immobilised. An example of an HRTF obtained from such a preparation is shown in Fig.4.8. Gain in the 2kHz-4kHz is 2dB-4dB higher than normal but no increases comparable with those accompanying microphone insertion (Fig.4.7) are apparent. For comparison, an HRTF obtained under meatus-blocked conditions is also reproduced in Fig.4.8. Before coating the TM with cyanoacrylic cement, the TM of this preparation was punctured and sample HRTF's obtained. One such sample is shown in Fig.4.8. The loss of gain at higher frequencies is understandable since under these circumstances the probe is probably monitoring SPL's in the bulla cavity as a whole. The increase in gain at 2kHz may possibly be the result of a resonance in the now acoustically coupled tympanic bulla and meatus.

These findings indicate that changing the shape of the termination of the ear canal, either by inserting a microphone or by puncturing the TM, appears to induce a canal-based resonance. The acoustic impedance of the TM itself does not appear to be such a critical factor in this respect.

4.6. Changing the Length of the Meatus.

The effective length of the meatus was changed by removing the TM and tympanic bulla and gluing (cyanoacrylic cement) a polythene tube of 4cm length into the cut proximal end of the meatus. The internal diameter

of the tube was about 3mm which allowed a 1/8 inch microphone to be slid up and down inside the tube whilst retaining an effective acoustic seal. The effectiveness of the seal had been previously checked by blocking the open end of the tube in the free-field. The polythene tube was of similar cross-section to the part of the meatus into which it was glued and reflections from the cut end of the polythene tube were therefore assumed to be minimal. Changing the position of the microphone in the polythene tube therefore changed the effective "acoustic length" of the meatus. The aim of this procedure was to produce a strong meatus-associated standing wave resonance and to identify it in the HRTF by shifting it up and down the frequency spectrum. Fig.4.9 shows sample spectra obtained from RP9, one of 3 animals investigated in this way. Insertion of the tube and microphone into the meatus results in peaks in the HRTF's at frequencies that are inversely correlated with the length of the tube. Thus for the 3cm tube (Fig.4.9(a)), peak gain of 36dB occurs at 1.75kHz, whereas for the 2cm tube, peak gain occurs at 2.0kHz-2.4kHz. For the 0.8cm tube (Fig.4.9(b)), peak gain occurs at 3kHz-4.0kHz, whereas when the meatus is effectively shortened by 0.7cm, there is no obvious increase in HRTF gain, although it may lie obscured in the higher frequency region of the HRTF. Peaks at higher frequencies also shift frequency as tube length is altered, and in some cases the peaks approximate to harmonics of the "meatus" resonance (e.g. the 3cm HRTF, Fig.4.9(a)).

Figure 4.9: HRTF's obtained at 0° azimuth, 0° elevation using a 1/8 inch microphone in a polythene tube of the following lengths:
(a) _____ 3cm and ..... 2cm.
(b) _____ 0.8cm and ..... meatus shortened by 0.7cm. (From RP9, cadaver head, left pinna facing 15° azimuth.)

Figure 4.10: HRTF's at 100° azimuth, 0° elevation:
_____ pinna intact.
..... tragus removed. (From RP10, cadaver, left pinna facing 18° azimuth.)

Fig. 4.9

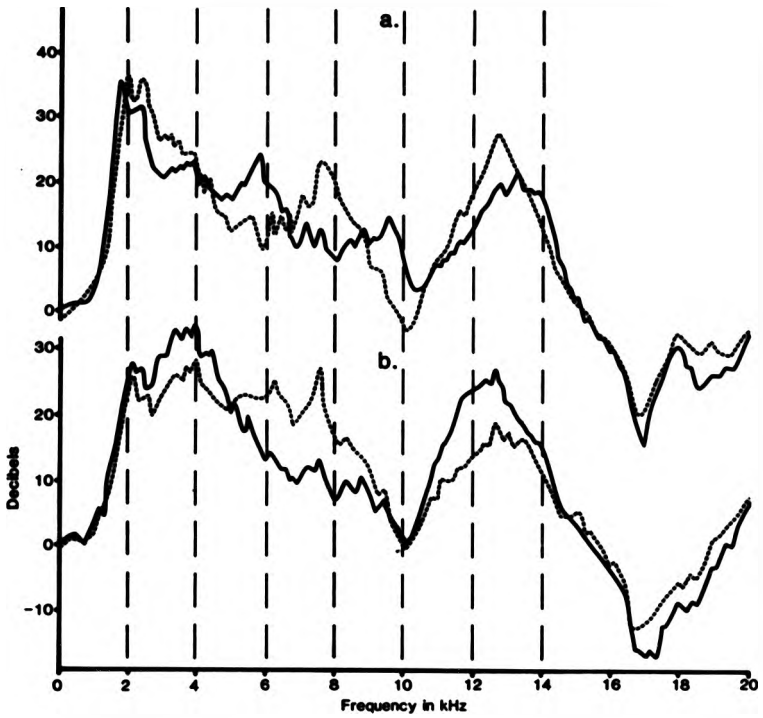
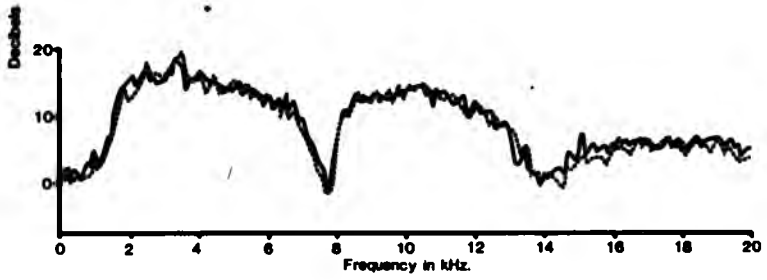


Fig. 4.10



However, harmonics of the low frequency resonance at 2.1kHz (which does not shift frequency with changing tube length) and the null at 10kHz, tend to obscure the "meatus" harmonic series.

Normal HRTF's for RP9 obtained from the living animal are shown in Fig.3.6(a). While the peak at 2.1kHz is a consistent feature of both sets of spectra, there is no sign of any region of gain attributable to a meatus-associated resonance. The 2.1kHz peak does not shift frequency with changing tube length and cannot therefore be associated with the meatus.

4.7. Experiments on the Tragal Notch.

Between the tragus and anti-tragus of the rabbit lies a distinct notch, about 1.5mm wide and 7mm long (measurements based on a 10cm length pinna). The notch is covered by fur in the living rabbit and is not readily visible. The acoustic significance of this notch was investigated by both blocking it and widening it.

Blocking experiments were carried out while monitoring the CM, and during the RP (probe insertion) series. The tragal notch was blocked by applying a suitably shaped piece of plasticene to the notch and ensuring adhesion to the tragus and anti-tragus. On no occasion could any difference be found between HRTF's obtained from normal and tragus-blocked preparations. Blocking the tragus has no effect on the HRTF.

The tragal notch was widened by about 4mm by removing the

tragus. This was carried out on 2 occasions with the same result; the low frequency HRTF peak shifted up-frequency by about 0.2kHz (Fig.4.10). This change was small but consistent for all HRTF's and it is clear that the tragus is necessary for the acoustic integrity of the concha; removing the tragus is equivalent to shortening the concha by about 4mm.

The function of the tragal notch remains unclear, but it appears not to lie in the frequency/intensity domain.

4.8. The Fossa and Anterior Pinna Fold.

The anterior pinna fold forms a longitudinally orientated cavity on the leading edge of the rabbit pinna which ends within the concha volume as a distinct pocket, the fossa. Blocking the fossa was carried out on 4 occasions by dropping a 5mm diameter ball of plasticene into it. This technique was adopted in order to minimise disturbance to the pinna. The results of this manoevre were variable; on two occasions no changes were apparent in HRTF's, but on two other occasions, there were up-frequency shifts in some of the HRTF nulls. Fig.4.11. shows two sets of HRTF's where this was observed. The variability in the results of the fossa blocking experiments may possibly be explained by the fact that inserting the ball of plasticene occasionally caused a slight, undetected re-orientation of the pinna.

The fossa is associated with the anterior pinna fold, and it was therefore decided to investigate the effects of

Figure 4.11: HRTF's obtained with

pinna normal _____,

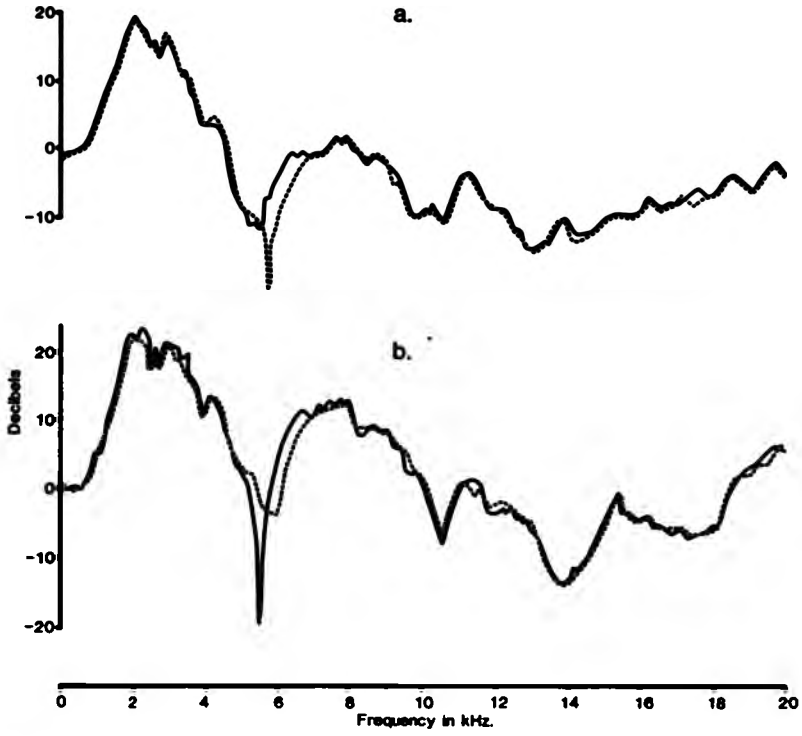
and fossa blocked ..... , at:

(a) 240° azimuth, 0° elevation,

(b) 120° azimuth, -40° elevation. (From RP8

cadaver head, left pinna facing 60° azimuth.)

Fig. 4.11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Frequency in kHz.

removing the latter. A number of effects of pinna fold removal were found, notably the formation of stronger nulls in anterior-ipsilateral HRTF's. (Fig.4.12). Examination of HRTF's at other elevations (e.g.-20°) also revealed that there was a general up-frequency shift in the low frequency nulls (Fig.4.13). It was also clear that the sound-collecting efficiency of the pinna had been affected by the removal of the anterior pinna fold; substantial loss in HRTF gain had occurred. In RP10 (right ear), and also RP9, the loss in gain was greatest for anterior/ipsilateral angles (Figs.4.12 and 4.13) although it was also high for contralateral angles, particularly in the 4kHz region. In RP10 (left ear) loss of gain was greatest at more posterior ipsilateral angles of azimuth, but an up-frequency shift of the low frequency HRTF nulls was also found in this data set.

Removal of the anterior pinna fold thus affects the gain of the HRTF and (as in some of the fossa blocking experiments) the frequency position of nulls.

4.9. The HRTF Nulls

Sharp minima or covert minima in the HRTF are referred to as nulls because they are frequency regions where SPL's in the recorded ear tend to approach 0dB. They can be distinguished from other minima by their sharpness and are probably the result of destructive interference at the mouth of the pinna or at the entrance to the meatus. The

latter appears to be the case in the human (Kuhn,1987), where the likely cause is interference between reflected and incident sound (on-axis) or between two sets of diffracted sound waves (off-axis). Destructive interference occurs when the coincident sound waves approach a phase difference of 180° and one would therefore expect nulls to occur in a 1/2 wavelength harmonic series. The frequency distribution of HRTF nulls for one rabbit is shown in Fig.4.14. Nulls are not a consistent feature of the HRTF and there are numerous gaps in the distribution patterns because of this. Nulls are rare at the contralateral angles for -20° and -40° elevation (Fig.4.14(c) and (d)) probably because of the diffraction resulting from the rabbit's body and the platform on which it was mounted.

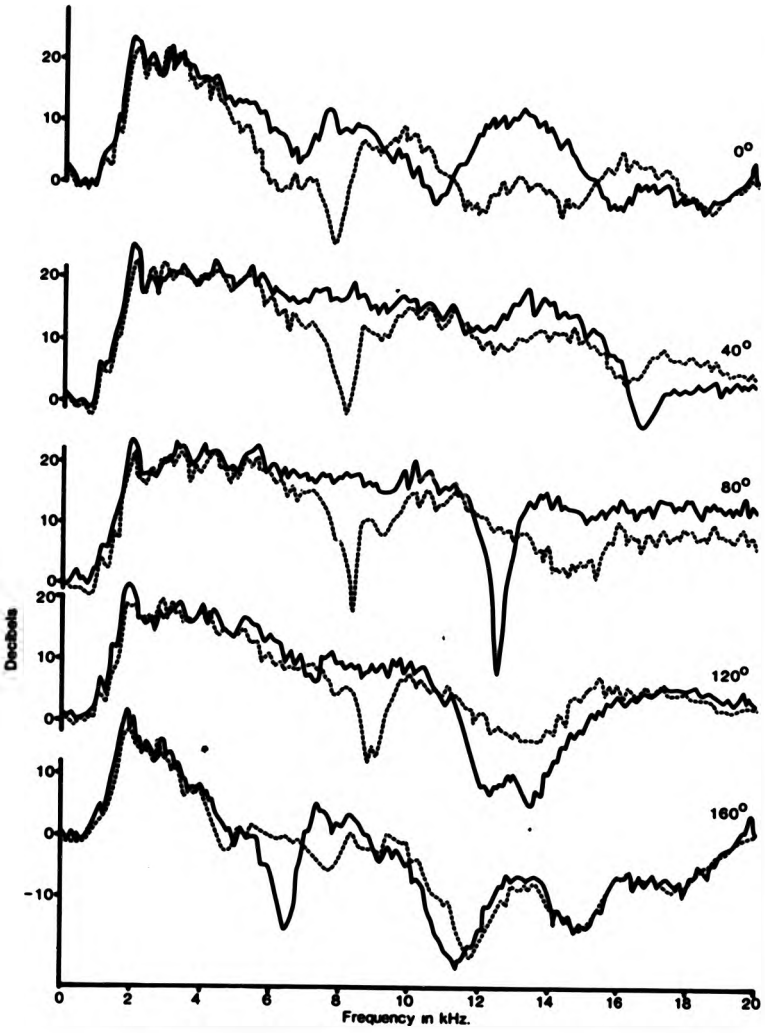
Nulls are also not commonly found when the sound is directly incident to the pinna mouth. Thus, the on-axis HRTF's at 0° elevation and above, tend not to show distinct nulls as such. However, small but sharp depressions do sometimes occur and, because of their position and regularity, they are assumed to be incipient nulls and have been included in Fig 4.14. At any one angle of azimuth, ipsilateral/anterior HRTF nulls tend to occur at a fixed frequency (e.g. Fig.4.14(b)) but then shift down-frequency for posterior and contralateral positions of the sound source. The nulls also shift frequency as the elevation of the sound source is changed. This was shown in chapter 3, and comparison of the frequency positions of the nulls in Fig.4.14 will confirm this.

Figure 4.12: HRTF's obtained at 0° elevation at various angles of azimuth:

_____ pinna intact,

..... anterior pinna fold removed. (From RP10 cadaver head, right pinna facing 50° azimuth.)

Fig. 4.12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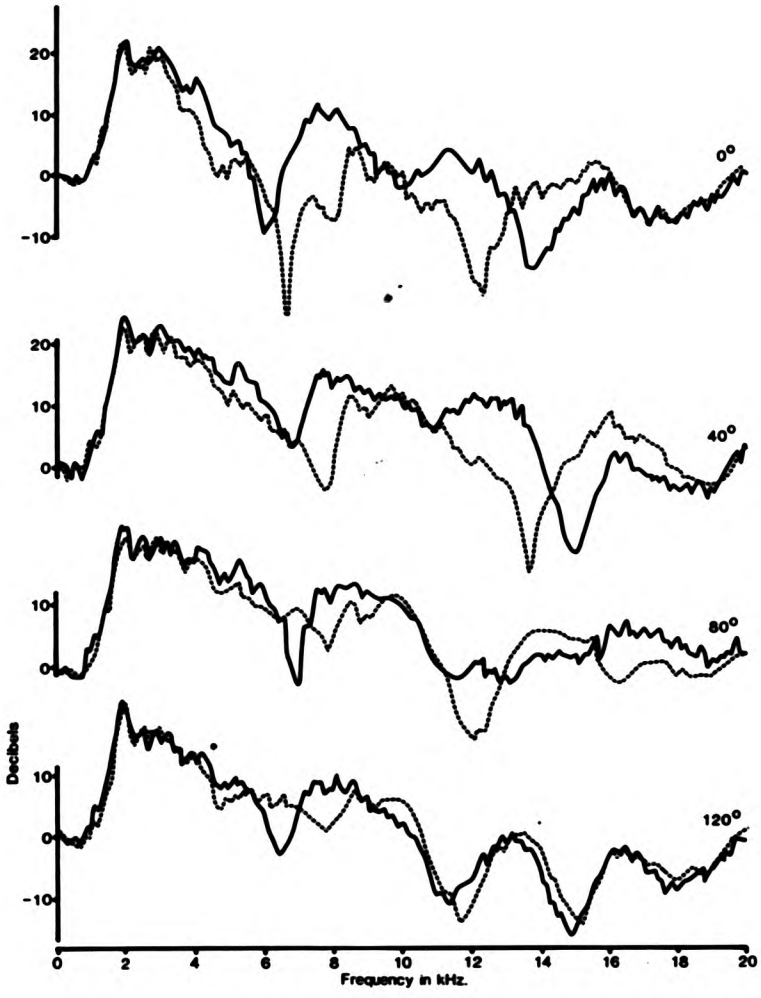
18
20
Frequency in kHz.

Figure 4.13: HRTF's obtained at -20° elevation at various angles of azimuth:

_____ pinna intact.

..... anterior pinna fold removed. (From RP10 cadaver head, right pinna facing 50° azimuth.)

Fig. 4.13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Decibels
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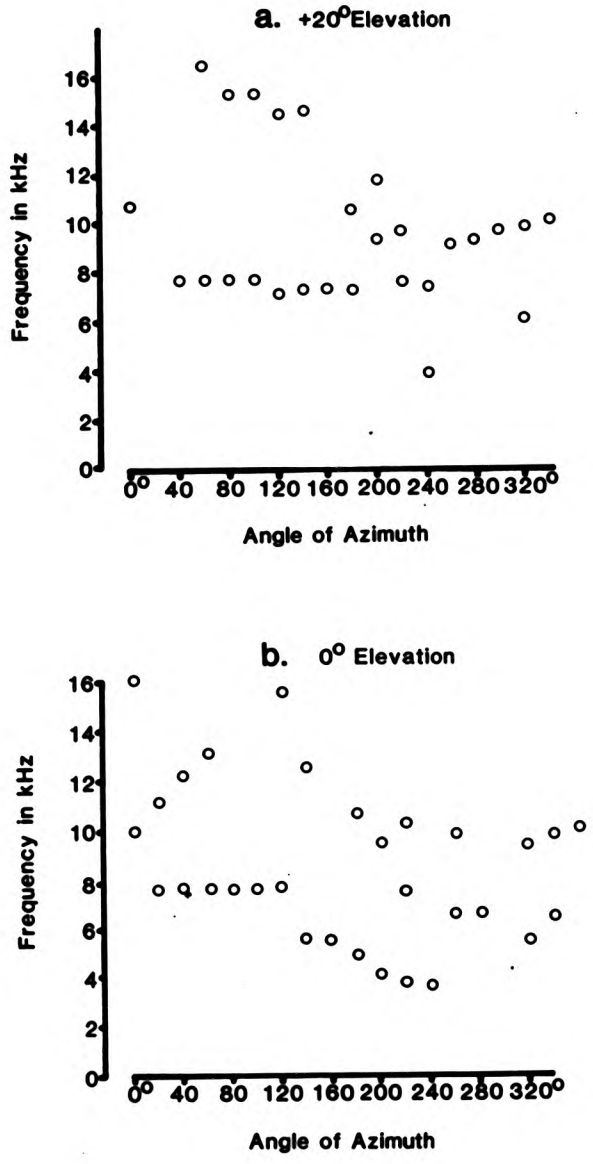
Frequency in kHz.

Figure 4.14: the frequency position of HRTF nulls at various angles of azimuth;
(a) at +20° elevation,
(b) at 0° elevation,
(c) at -20° elevation,
(d) at -40° elevation. (From RP10, living, left pinna facing 18° azimuth.)

Fig. 4.14


a. +20° Elevation
Frequency in kHz
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0° 40 80 120 160 200 240 280 320°
Angle of Azimuth
b. 0° Elevation
Frequency in kHz
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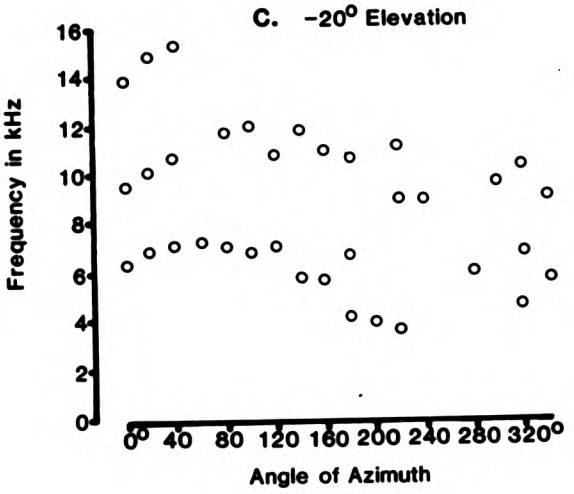
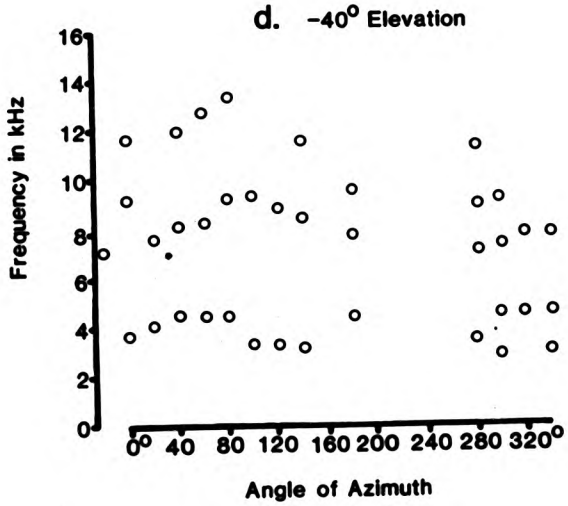
0° 40 80 120 160 200 240 280 320°
Angle of Azimuth

Fig. 4.14 cont'd.





The strongest nulls occur at -20° and -40° elevation, but clear evidence that the nulls approximate to a harmonic series is missing. Thus, for example, at -40° elevation, 40° azimuth (Fig.4.14(d)), nulls occur at 6.4kHz, 10.0kHz and 13.9kHz. However, if there had been a null at, say, 3.2kHz, this might be said to approximate to a 1/2 wavelength harmonic series. It could, therefore be argued that, for some of the ipsilateral HRTF's, the nulls occur at intervals that approximate to a harmonic series where the fundamental is obscured. However, there is little indication of "obscured" fundamentals at 0° elevation and above.

Removal of the anterior pinna fold results in loss in gain and the formation of deep nulls in the 7kHz-8kHz region of the 0° elevation HRTF's from 0° to 120° azimuth (see Fig.4.12). The anterior pinna fold thus appears to make a strong contribution to the anterior and lateral azimuthal HRTF's.

4.10. A Simple Model.

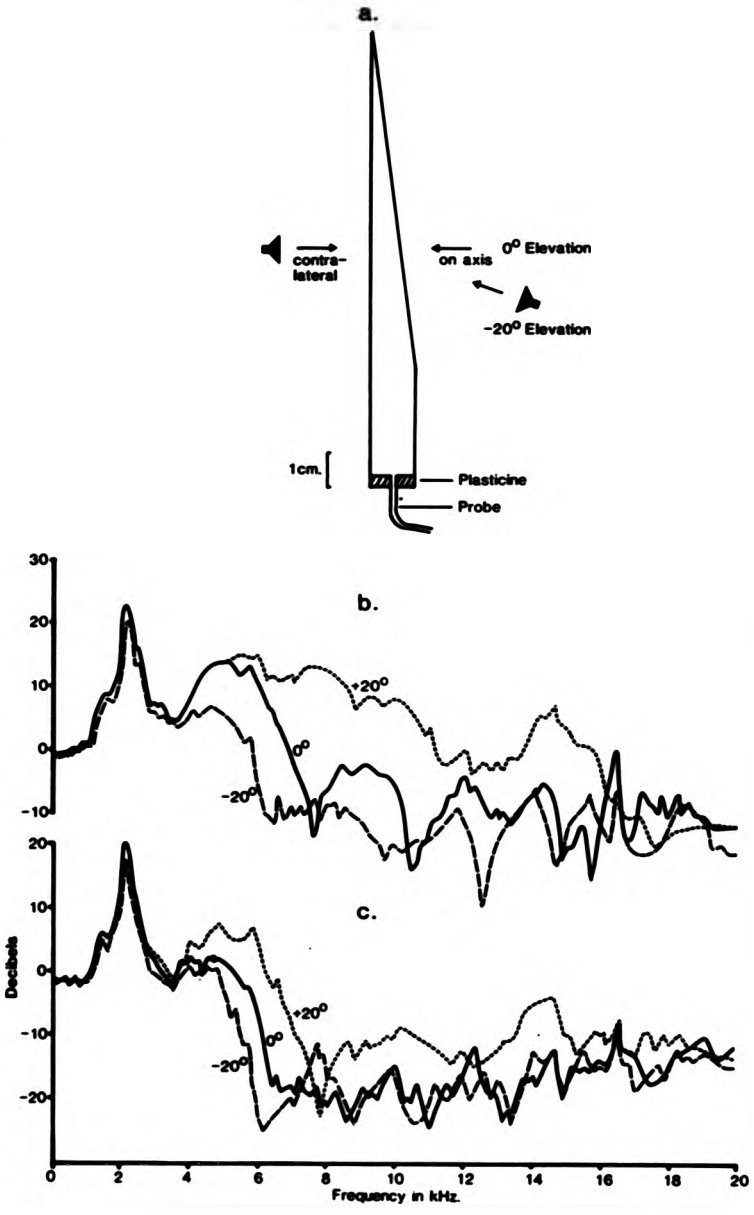
It has proved possible to simulate the pattern of null occurrence found for the rabbit external ear with a simple model. This consisted of a polythene tube of internal diameter 1.2cm, blocked at one end with a flat plasticene plug and cut obliquely at the open end (Fig.4.15(a)). The probe was positioned centrally in the plug with the tip flush with the internal surface. Sample transfer functions

obtained from this model (Fig.4.15) all show a peak at 2.2kHz which is the 1/4 wavelength fundamental depth resonance of the tube. This indicates that the effective depth of the tube is 3.9cm. The end correction of 0.9cm is larger than the "expected" 0.36cm (0.6 x tube radius) presumably because of the oblique open end of the tube. Sharp nulls occur in the transfer functions in the 6kHz-8kHz region both "on-axis" (Fig.4.15(b)) and "contralateral" (Fig.4.15(c)) to the tube opening. The nulls show a general tendency to shift up-frequency as the angle of elevation of the sound source is increased, although nulls are absent from the on-axis +20° elevation function. The contralateral transfer functions (Fig.4.15(c)) tend to develop nulls between 6kHz and 8kHz. The path-length difference required for a null to occur at 7kHz is 2.45cm. The actual path-length difference at the mid point of the model mouth for 0° elevation when the sound source is contralateral is 2.31cm (r+1/4circumference, based on external measurements of model; r=0.9cm.) This is a sufficiently good match to indicate diffraction around the model as a likely cause of the contralateral nulls. The on-axis null at 0° elevation occurs at 7.7kHz, indicating a path-length difference of 2.23cm between interacting sound waves. This is within 2 x diameter of the model and interaction between sound incident to, and reflected from, the pinna face is not ruled out.

The rabbit pinna is asymmetrical in both vertical and

Figure 4.15: (a) A scale drawing of the obliquely truncated tube used to model the pattern of null occurrence found for the rabbit pinna: (b) and (c) transfer functions obtained at 3 angles of elevation with the sound source (b) on-axis and (c) "contralateral" to the mouth of the tube.

Fig. 4.15


a.
contra-
lateral
on axis
0° Elevation
-20° Elevation
1cm.
Plasticine
Probe
b.
+20°
0°
-20°
c.
+20°
0°
-20°
Decibels
30
20
10
0
-10
-20
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

transverse section. The folds on the edge of the pinna, and the subdivisions of the concha bowl are further complications. Nevertheless, it may be possible to explain the HRTF nulls in relatively simple terms. The contralateral nulls appear to have their fundamentals in the 3kHz-4kHz region. This would mean a path-length difference of about 5.7cm-4.3cm. The circumference of the rabbit pinna at the mid-point of the pinna mouth is about 11cm (based on a pinna length of 10cm) reducing to 10cm below this level, which would indicate a path length difference of about between 5.5cm and 5.0cm.

On-axis nulls tend to appear at 7.5kHz (e.g. Fig.4.14(b)) indicating a path length difference of 2.29cm. This is approximately the depth of the pinna face and may indicate that sound reflected back from the pinna face is interacting with the incident sound.

This simple explanation of null formation in the rabbit HRTF does not take into account the role of the pinna folds, or the asymmetry of the pinna. Neither have the changes in null frequency position with changes in sound source position been dealt with in detail. An explanation of these details must await a more complex model.

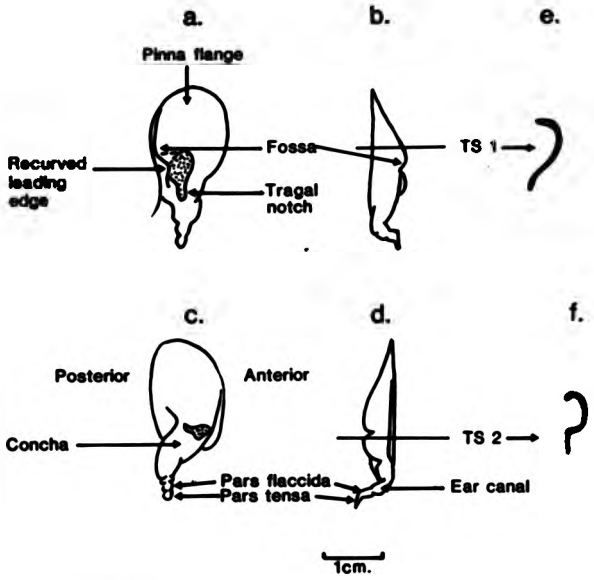
CHAPTER 5. RESULTS: THE RAT

5.1. Anatomy of the External Ear.

The relative sizes of the external ears of experimental subjects (Sprague-Dawley albino rats) were monitored by using the distance between the tip of the pinna and the base of the tragal notch as the standard measure of pinna length. These measures ranged from 1.9cm to 2.1cm and tended to correlate to subject weight. Endocasts of the external ears were made using casting plaster or silicon moulding rubber (Silastic E). The most complete fills of the external ear were obtained by introducing Silastic E under vacuum (760mm Hg for 2-3hrs) with a small hole bored in the base of the meatus. Figure 5.1 shows drawings of which (a) is a composite of an endocast and external view, while (b), (c) and (d) are drawn solely from an endocast; (e) and (f) were drawn from sections cut from the ear of a cadaver. The leading edge of the pinna is recurved while the rear edge is flat (Fig. 5.1(e) and (f)). There is a pocket in the pinna face; this has been termed the fossa because of its association with the leading edge of the pinna. The term "concha" has been used for the complex cavity below the level of the fossa. The ear canal enters the concha at a sharp angle (Fig. 5.1(b) and (c)) and in turn bends sharply as it enters the cavity housing the TM. The TM is composed of a pars flaccida and a slightly larger pars tensa (see Fig. 5.1(c)), and forms the medial wall of the terminal part of the ear canal. Measurements from an endocast of an external ear of pinna length 2.0cm were as

Figure 5.1: Drawings of the left external ear of the rat: (a) on-axis view of a composite of external view and endocast. (b) view of trailing edge of endocast. (c) contralateral view of endocast,
(d) view of leading edge of endocast.
(e) transverse section of ear at level indicated in (b). (f) Transverse section of ear at level indicated in (d).

Fig. 5.1


a.
b.
e.
Pinna flange
Fossa
TS 1
Recurved leading edge
Tragal notch
c.
d.
f.
Posterior
Anterior
Concha
TS 2
Pars flaccida
Pars tensa
Ear canal
1cm.

follows: ear canal length was 7mm; ear canal diameter at the entry point to the concha was 3.5mm and the diameter at the entry to the portion housing the TM was 1.9mm; the concha depth (top of tragal notch to ear canal entrance) was 7mm.

5.2 Directional Characteristics of the External Ear.

Azimuthal dependence functions at 0° elevation were obtained from 3 cadavers by means of probe implant in the base of the meatus, and from 2 living animals by monitoring the cochlear microphonic. Frequencies above 20kHz were strongly attenuated by the head and pinna when the sound source was off-axis to the recorded pinna and consequently the azimuth dependence functions were limited to 20kHz and below. A typical series of azimuthal dependence functions at 0° elevation is presented in Fig.5.2. The main lobe of each function is generally at, or around, 60° azimuth which was the angle faced by the pinna during data collection. A covert maximum occurs at about 240° azimuth in the functions at higher frequencies (10kHz-20kHz). This is similar to the "bright spot" described for human azimuthal dependence functions (Shaw,1974).

The directional characteristics of 5 external ears are summarised in Fig.5.3 in terms of the -3dB acceptance angles of the main lobes of the azimuthal dependence functions. Overall, there is a gradual decrease in the acceptance angles with increasing frequency, but the

Figure 5.2: Azimuthal dependence functions at 0° elevation obtained from Rat Probe 3 using pure tones. Left pinna facing 60° azimuth.

Fig. 5.2

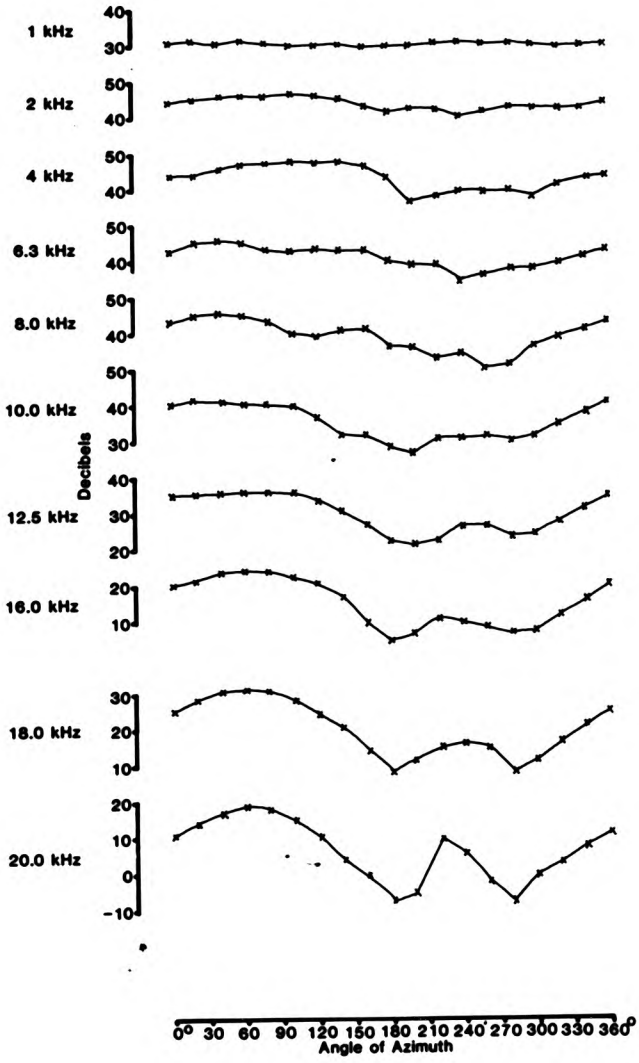
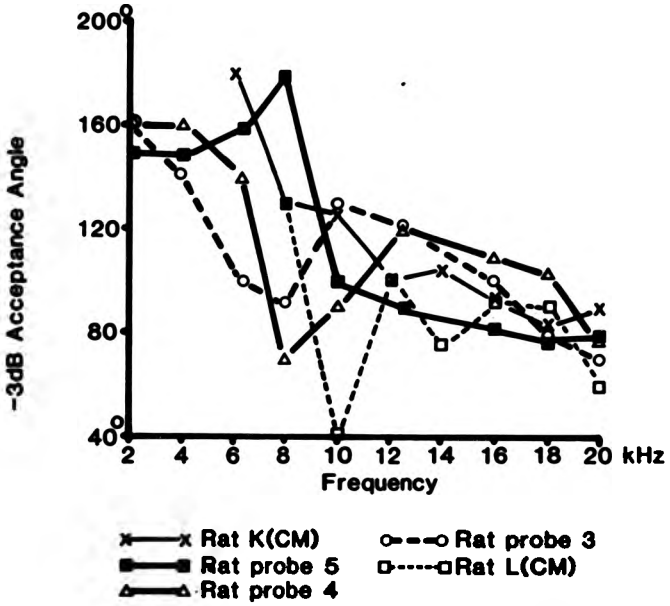

1 kHz
40
30
2 kHz
50
40
4 kHz
50
40
6.3 kHz
50
40
8.0 kHz
50
40
10.0 kHz
50
40
30
12.5 kHz
40
30
20
16.0 kHz
20
10
18.0 kHz
30
20
10
20.0 kHz
20
10
0
-10
Decibels
0° 30 60 90 120 150 180 210 240 270 300 330 360°
Angle of Azimuth

Figure 5.3: -3dB acceptance angles of the main lobes of azimuthal dependence functions obtained at 0° elevation plotted as functions of frequency for 5 rats. (From 3 probe implant and 2 CM studies.)

Fig. 5.3


200
160
120
80
40
-3dB Acceptance Angle
2
4
6
8
10
12
14
16
18
20 kHz
Frequency
Rat K(CM)
Rat probe 5
Rat probe 4
Rat probe 3
Rat L(CM)

functions for individual animals are non-monotonic. Three subjects show acceptance angles of 90° or less between 8kHz and 10kHz but increased acceptance angles at higher frequencies. At 20kHz, however, all 5 subjects show acceptance angles of between 90° and 60°.

5.3. Head Related Transfer Functions.

HRTF's were obtained from 5 cadavers by means of a probe implanted into the base of the ear canal. Anterior sector HRTF's at 0° elevation from 4 cadavers are shown in Fig.5.4. On-axis HRTF's (40° and 80° azimuth) generally show maximum gain of around 18dB between 6kHz and 8kHz, gain dropping substantially in 2 of the 4 sets of HRTF's (Fig.5.4 (a) and (c)) in the 17kHz region. A clearly atypical series of HRTF's is that shown by Rat Probe 5, (Fig.5.4(d)). This was a small (200gm) female of pinna length 1.9cm which on examination at the end of the experiment proved to have an infected middle ear. The HRTF's show gains of up to 8dB or 9dB above normal which are, presumably, the result of increased acoustic impedance of the TM.

A more complete series of HRTF's, from what is regarded as a typical preparation, is shown in Fig.5.5. Maximum gain of up to 20dB occurs at about 8.5kHz, a covert maximum of up to 17dB occurs at 13.5kHz and gain drops to 0dB at 19kHz-20kHz. Consistent differences in gain between ipsilateral HRTF's do not occur below 12kHz (Fig.5.5(a) and

Figure 5.4: Anterior-ipsilateral sector HRTF's at 0° elevation obtained from 4 cadavers (probe implants in the wall of the ear canal):
(a) Rat Probe 1, left pinna facing 25° azimuth,
(b) Rat Probe 2, right pinna facing 75° azimuth,
(c) Rat Probe 3, left pinna facing 60° azimuth,
(d) Rat Probe 5, left pinna facing 77° azimuth.

Fig. 5.4

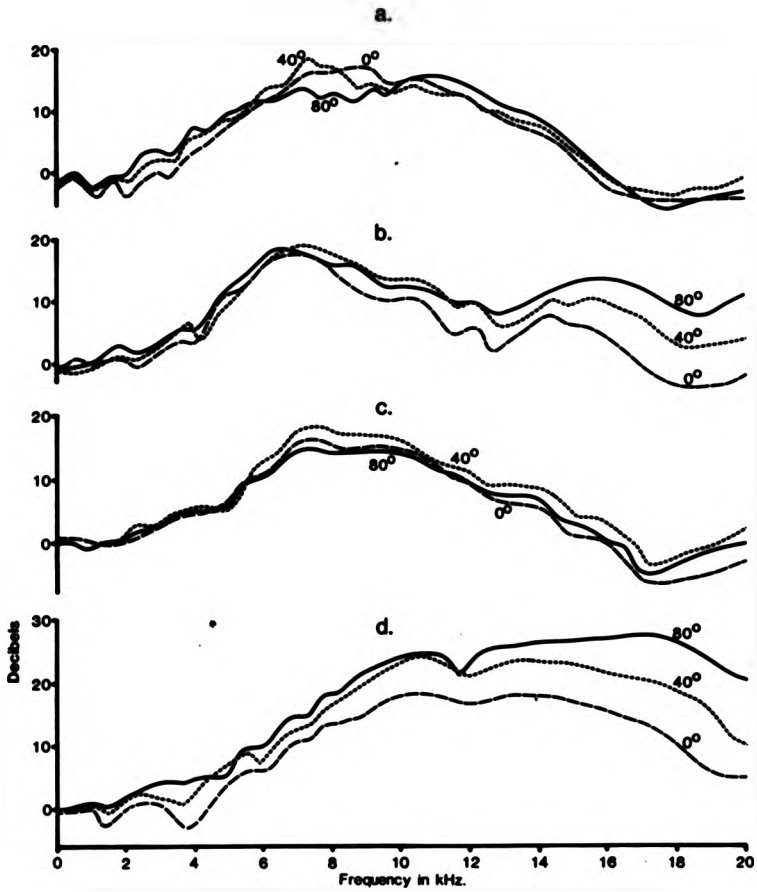

a.
40°
0°
80°
b.
80°
40°
0°
c.
80°
40°
0°
d.
80°
40°
0°
Decibels
0
10
20
30
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 5.5: HRTF's at 0° elevation from Rat Probe 4 (cadaver), left pinna facing 60° azimuth;
(a) anterior-ipsilateral sector,
(b) posterior-ipsilateral sector,
(c) contralateral sector.

Figure 5.6: HRTF's at 80° azimuth for various elevations; from Rat Probe 4 (cadaver), left pinna facing 60°.

Fig. 5.5

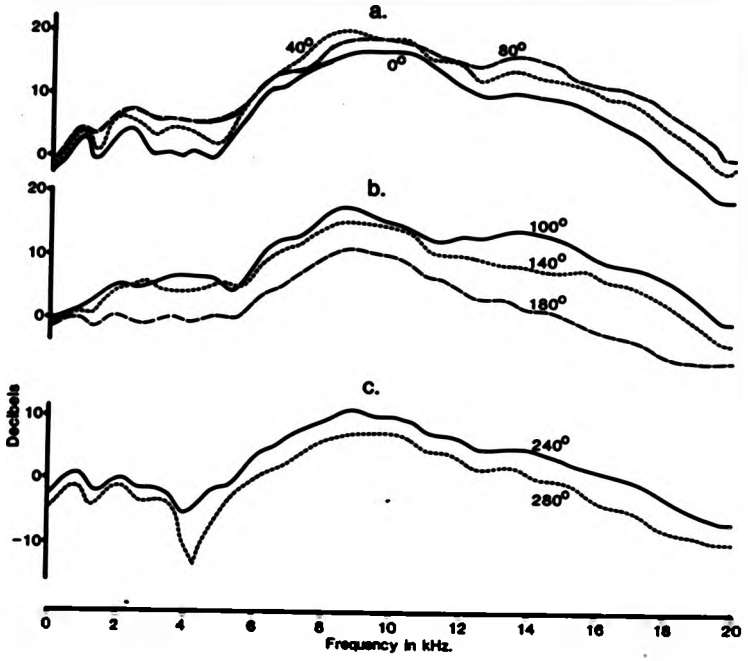
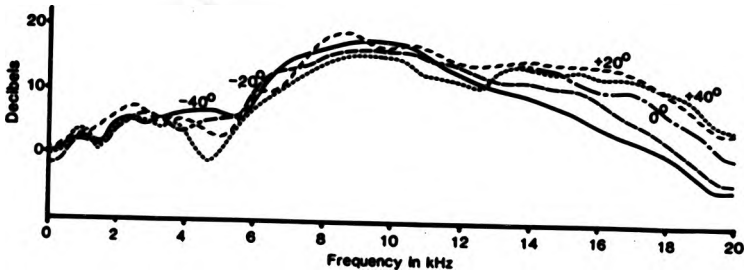

a.
40°
0°
80°
b.
100°
140°
180°
c.
240°
280°
Decibels
20
10
0
-10
0 2 4 6 8 10 12 14 16 18 20
Frequency in kHz.

Fig. 5.6


Decibels
20
10
0
-40°
-20°
+20°
+40°
0°
0 2 4 6 8 10 12 14 16 18 20
Frequency in kHz

(b)). HRTF nulls occur only at contralateral angles in the 4.5kHz region (see Fig.5.5(c)). A series of HRTF's at different angles of elevation are shown in Fig.5.6. Above 12kHz there is a progressive increase in gain with increasing elevation up to about +40°.

5.4. Cochlear Microphonic Recordings.

CM recordings were obtained from 13 rats using the technique described in Chapter 2. For the majority of subjects, the largest CM's obtained were in the region of 200uV but CM's of more than 400uV were obtained from 2 subjects. The reason for this variability was that the round window was obscured by a shelf of bone and the recording electrode had to be positioned by trial and error. Recording electrode positions were therefore likely to have been variable. CM spectra were recorded on an instrumentation recorder and played back at half speed thus enabling high resolution signal analysis from 100Hz-40kHz.

The relationship between signal level and CM amplitude depended on whether pure tones or broad-band sound were employed as the signal. Figure 5.7 shows this relationship for Rat I (CM's up to 480uV) at 3 frequencies. The best ratio of CM amplitude / signal level was about 0.94 for pure tones whereas the best ratio obtained using broad-band sound (40dB-20dB attenuation at 16kHz) was 0.73. Fig.5.8 shows examples of CM / signal amplitude relationship for Rat L (CM's up to 150uV); the best ratio obtained using

Figure 5.7: Relationship between signal SPL and CM amplitude for Rat I:
(a) Pure tones.
(b) measurements taken from CM spectra obtained using broad-band sound.

Figure 5.8: Relationship between signal SPL and CM amplitude for Rat L:
(a) pure tones.
(b) measurements taken from CM spectra obtained using broad-band sound.

Fig. 5.7

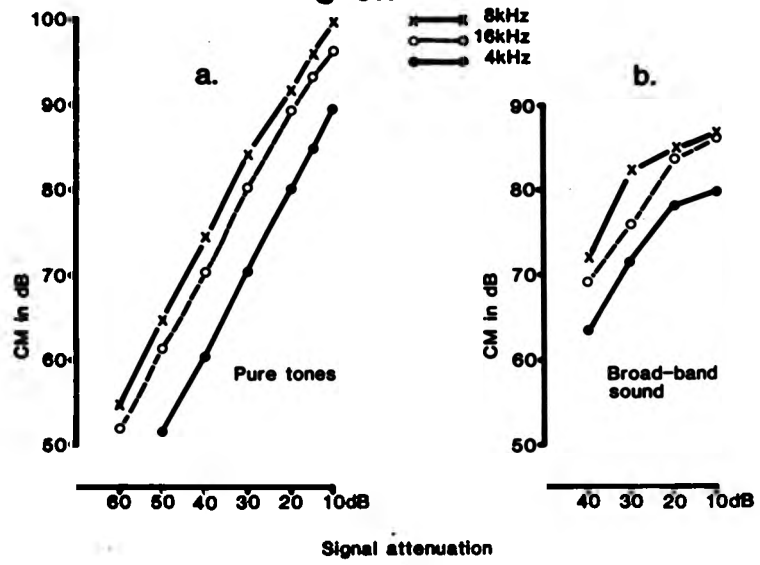
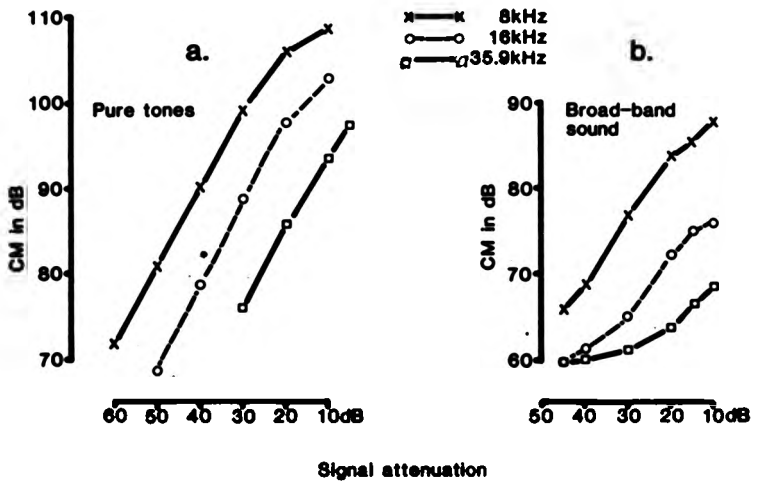

8kHz
16kHz
4kHz
a.
b.
100
90
80
70
60
50
CM in dB
Pure tones
Broad-band sound
60 50 40 30 20 10dB
40 30 20 10dB
Signal attenuation

Fig. 5.8


8kHz
16kHz
35.9kHz
a.
b.
110
100
90
80
70
60
CM in dB
Pure tones
Broad-band sound
60 50 40 30 20 10dB
50 40 30 20 10dB
Signal attenuation

pure tones was 0.96 and the best ratio for broad-band sound was 0.76. The stability of the CM was monitored by recording the CM spectrum at 0° elevation, 40° azimuth at various stages throughout each experiment. While the CM remained relatively stable over short periods of time, from the beginning to the end of each experiment there was usually a change in the CM. The largest changes tended to occur in the 12kHz to 32kHz range and were typically about 3dB, although changes (and they could be gains or losses) of up to 6dB occurred in some cases.

Sample CM spectra (at 0° elevation) from one of the most sensitive (Rat I) and one of the least sensitive (Rat L) preparations are shown in Figs.5.9 and 5.10 respectively. The CM spectra at different angles of azimuth show increasingly-strong separation from about 12kHz, particularly in the anterior-ipsilateral sector (Fig.5.9(a) and Fig.5.10(a). CM spectra from other preparations show the same trend but the extent of separation is generally below that shown by the CM spectra obtained from Rat I. Spectra obtained from the posterior-ipsilateral sector (Fig.5.9(b) and Fig.5.10(b)) show smaller degrees of separation than the anterior-ipsilateral spectra. This was not found to be the case in the rat probe studies (see Fig.5.5). Apart from this the findings of the CM studies confirm those of the probe implant studies.

Directional sensitivity in the ipsilateral sector appears to be maintained up to about 30kHz. Above this frequency CM spectra in the ipsilateral sector tend to drop below noise

Figure 5.9: CM spectra at 0° elevation from Rat I, (left pinna facing 54° azimuth):

(a) anterior-ipsilateral sector,

(b) posterior-ipsilateral sector,

(c) contralateral sector.

Fig. 5.9

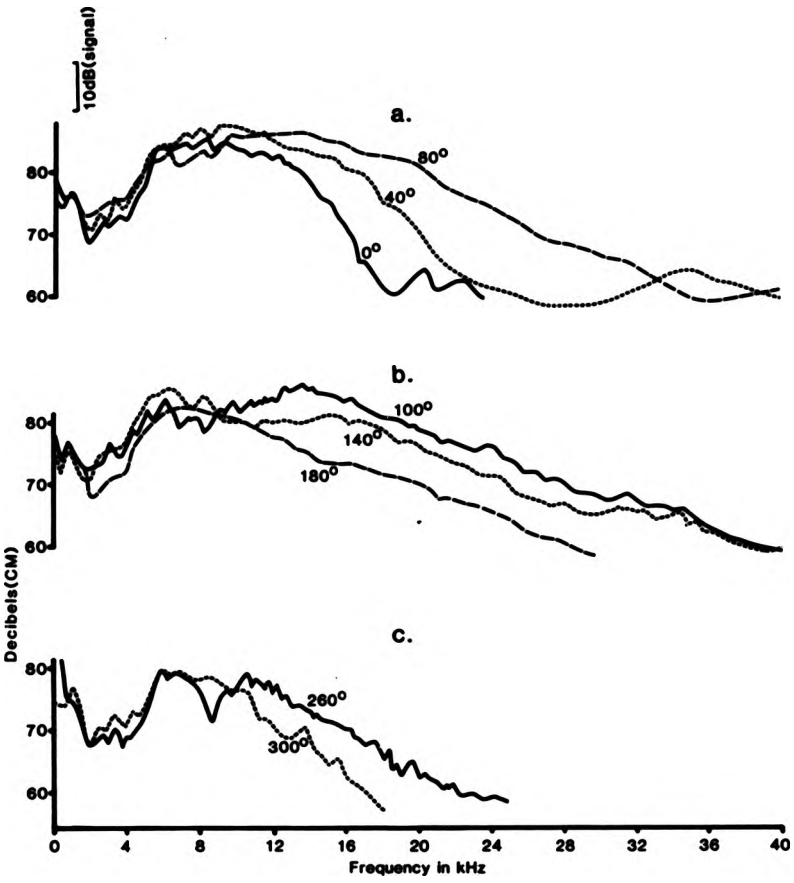
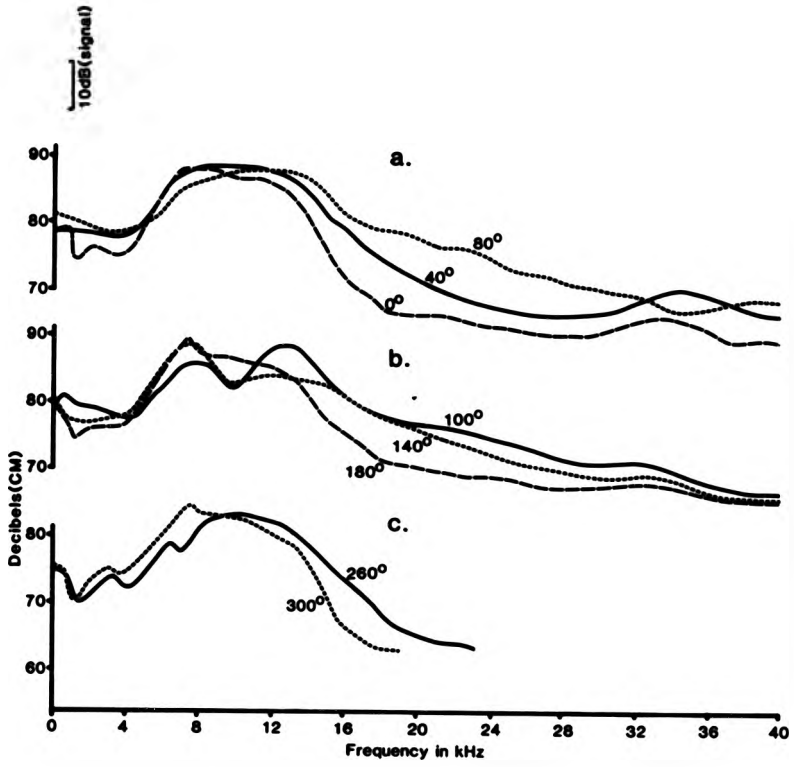

10dB(signal)
a.
80°
40°
0°
b.
100°
140°
180°
c.
260°
300°
80
70
60
Decibels(CM)
0
4
8
12
16
20
24
28
32
36
40
Frequency in kHz

Figure 5.10: CM spectra at 0° elevation from Rat L. (left pinna facing 55° azimuth):
(a) anterior-ipsilateral sector.
(b) posterior-ipsilateral sector;
(c) contralateral sector.

Fig. 5.10


10dB(signal)
a.
b.
c.
80°
40°
0°
100°
140°
180°
260°
300°
Decibels(CM)
90
80
70
60
0
4
8
12
16
20
24
28
32
36
40
Frequency in kHz

levels but, from general acoustical principles, it would seem likely that directional sensitivity is maintained up to the upper frequency limits of the animal's hearing. CM spectra obtained from the contralateral sector (Figs.5.9(c) and 5.10(c)) tend to drop below noise levels at, or around, 20kHz.

A series of CM spectra obtained with the sound source at different elevations is shown in Fig.5.11. The spectra show progressive increases in gain with increasing elevation of the sound source. Ipsilateral spectra show these changes at higher frequencies than do contralateral spectra. Thus, at 40° azimuth, these changes occur over the 16kHz-28kHz range (Fig.5.10(a)) whereas at 320° azimuth the changes occur between about 12kHz and 22kHz (Fig.5.10(b)). Similar trends were shown by CM spectra obtained from other preparations.

5.5. Interaural Intensity Differences.

IID spectra were obtained from 2 cadavers using implanted probes and from 13 living rats by monitoring the CM. IID spectra were obtained at every 10° or 20° azimuth for every 20° of elevation from -20° to +80° elevation. A series of IID spectra obtained using a probe implant in a cadaver is shown in Fig.5.12. The contralateral spectra obtained with this specimen, as with most probe implants, tended to drop below noise levels at around 16kHz and above. Nevertheless, the IID spectra in the anterior sector show changes of up to 0.3dB per 1° of azimuth (0°-60° azimuth). IID spectra

Figure 5.11: CM spectra at various elevations from Rat I. (left pinna facing 54° azimuth):
(a) at 40° azimuth.
(b) at 320° azimuth.

Figure 5.12: IID spectra at 0° elevation from Rat Probe 3. (left pinna facing 60° azimuth):
(a) anterior sector.
(b) posterior sector.

Fig. 5.11

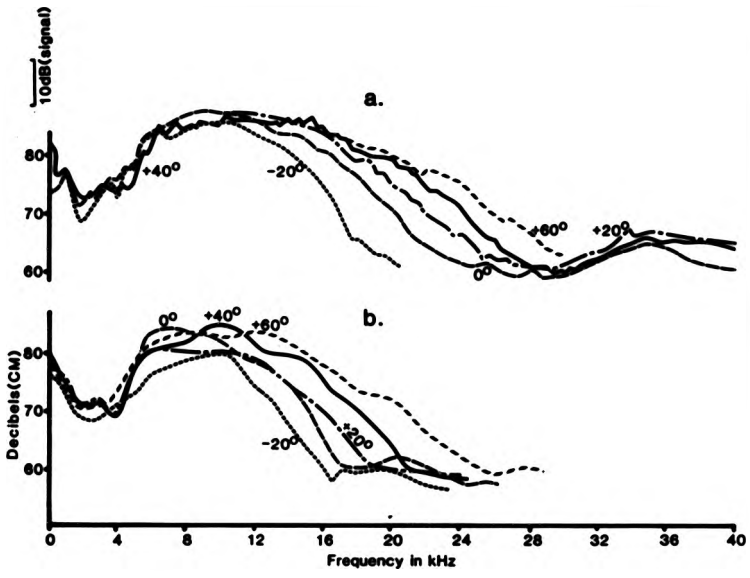
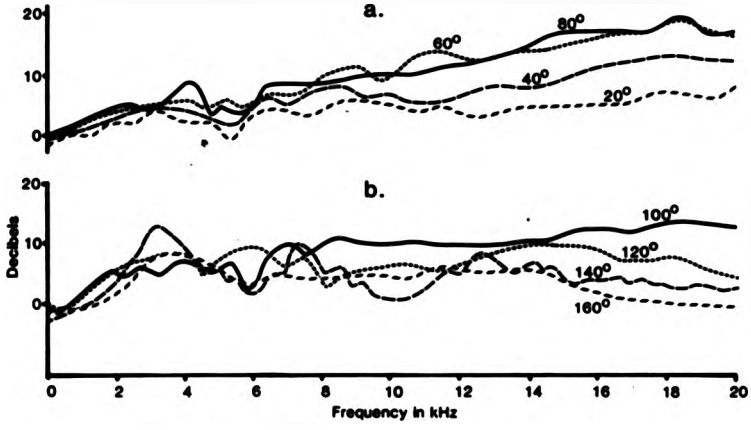


Fig. 5.12



obtained from the posterior sector (Fig. 5.12(b)) show smaller changes than this and over a more restricted frequency range. Lateral sector IID's (60°, 80° and 100°) do not show good separation.

A series of IID spectra at 0° elevation obtained using the cochlear microphonic is shown in Fig.5.13. In the anterior sector (Fig.5.13(a)), there is an orderly progression of spectra with angle of azimuth which obtains from 8kHz to 28kHz. This holds true for the posterior sector (Fig.5.13(b)) also, except that the ordering extends to even higher frequencies. The reason for this is that spectra obtained from the anterior-contralateral sector tend to drop below noise levels at around 20kHz. Anterior sector IID spectra thus are underestimates of the IID's actually available to the conscious rat at frequencies above 20kHz.

IID value changes exceed 0.5dB per 1° of azimuth at 17kHz (0°-60° azimuth) for Rat I (Fig.5.13). Rat I was unusual, however, in both the sensitivity of the CM (up to 480uV) and in the directional sensitivity of the CM spectra obtained from it. IID spectra from Rat L, one of the least sensitive preparations (maximum CM of 150uV), are therefore shown for comparison in Fig.5.14. IID values changed at the rate of 0.3dB per 1° azimuth at 17kHz (0°-60° azimuth) for this preparation.

CM IID spectra obtained at different angles of elevation do not show progressive changes in magnitude; IID's at 0° elevation tend to be the largest. The IID spectra do,

Figure 5.13: CM IID spectra at 0° elevation from Rat I. (left pinna facing 54° azimuth):
(a) anterior sector.
(b) posterior sector.

Figure 5.14: CM IID spectra at 0° elevation from Rat L. (left pinna facing 55° azimuth):
(a) anterior sector.
(b) posterior sector.

Fig. 5.13

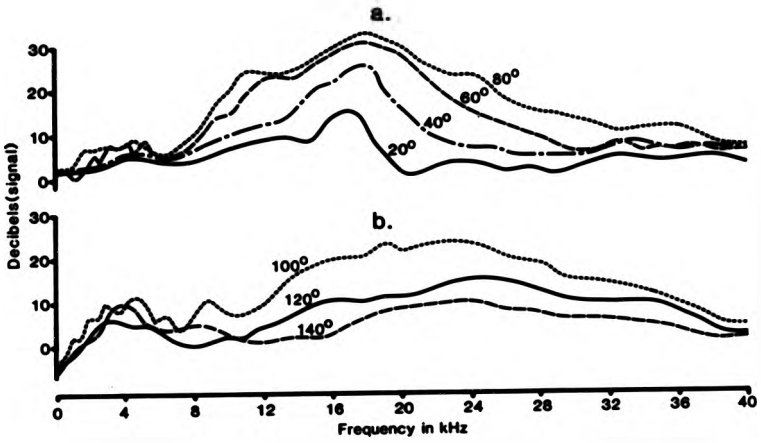
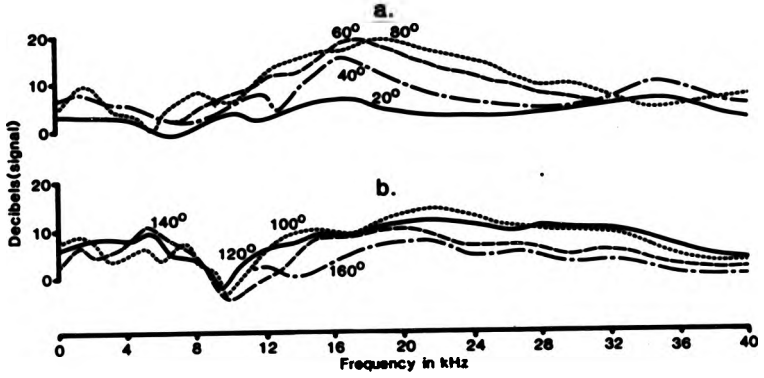


Fig. 5.14



however, show progressive up-frequency shifts in spectral features with increasing sound source elevation. Fig.5.15 shows a series of IID spectra for various elevations at 60° azimuth. There is a gradual up-frequency shift in the main peak with increasing elevation. This is the result of the similar trends shown by CM spectra, but where contralateral changes occur at lower frequencies than ipsilateral changes (see Fig.5.11). A similar series of IID spectra obtained at various elevations at 40° azimuth is shown in Fig.5.16. The progressive up-frequency shift of IID spectrum features with increasing sound source elevation was shown by all subjects, but was at its clearest in CM studies where it was possible to monitor frequencies above 20kHz.

IID's plotted as functions of azimuth (Fig.5.17) generally show monotonic increases with increasing angle of azimuth in the anterior sector. For pinnae facing antero-laterally, peak IID values tend to occur around 80° azimuth. IID functions tend to be non-monotonic in the posterior sector. IID functions at different frequencies clearly show the tendency to increased directionality above 12kHz. IID's are thus useful localisation cues in the anterior sector primarily, and one would expect directional acuity to increase with increasing frequency of the signal.

5.6. Pinna Flange Removal.

The 3-4mm wide strip of tissue around the rim of the pinna, referred to here as the pinna flange, was removed during 4 probe implant experiments. The flange (and this

Figure 5.15: CM IID spectra at various elevations from Rat I at 60° azimuth, (left pinna facing 54° azimuth).

Figure 5.16: CM IID spectra at various elevations from Rat L at 40° azimuth, (left pinna facing 55° azimuth).

Fig. 5.15

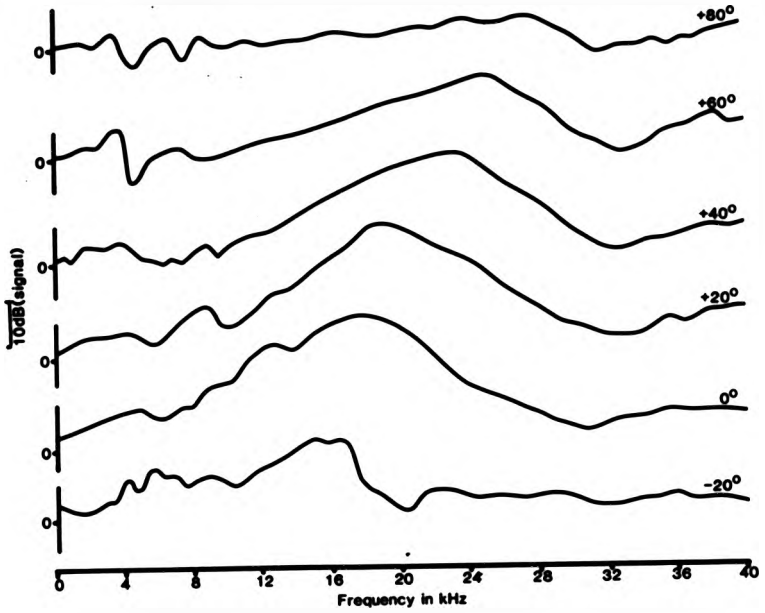


Fig. 5.16

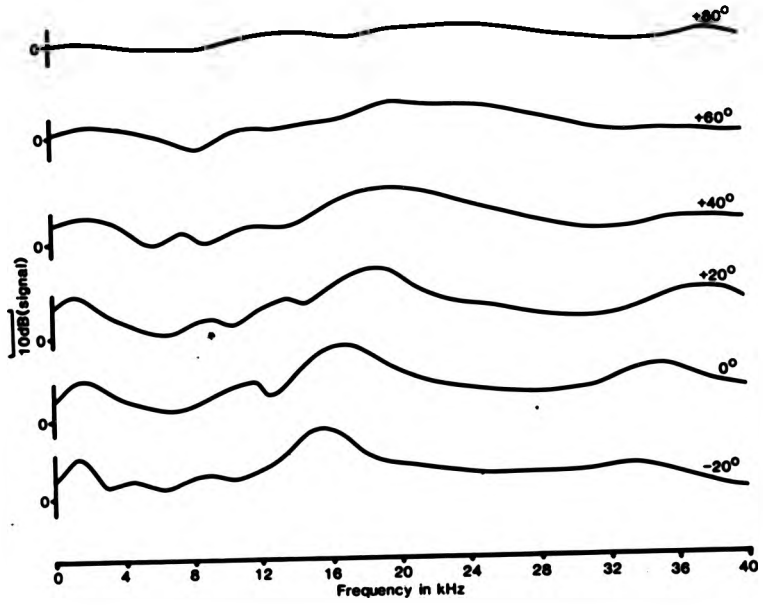
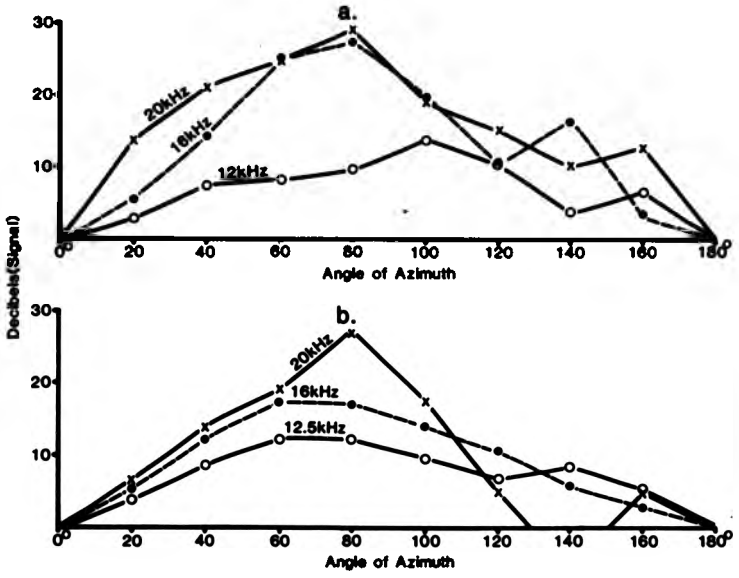


Figure 5.17: IID's calculated from azimuthal dependence studies using pure tones at 0° elevation. IID's for various frequencies are plotted as functions of azimuth;
(a) from Rat K, (CM study, left pinna facing 50° azimuth),
(b) Rat Probe 3, (cadaver, right pinna facing 60° azimuth).

Fig. 5.17


a.
30
20
10
20kHz
16kHz
12kHz
0°
20
40
60
80
100
120
140
160
180°
Angle of Azimuth
Decibels(Signal)
b.
30
20
10
20kHz
16kHz
12.5kHz
0°
20
40
60
80
100
120
140
160
180°
Angle of Azimuth

includes both the recurved leading edge and the trailing edge of the pinna) was cut off with a pair of scissors with the cadaver in situ in the anechoic chamber, care being taken not to disturb the orientation of the ear. On-axis to the sound source (Fig 5.18, HRTF's at 80° azimuth), pinna flange removal resulted in a general loss in gain, (up to 9dB), the loss tending to increase with increasing frequency. At angles of azimuth contralateral to the sound source, pinna flange removal also resulted in some loss of gain (see Fig.5.18, HRTF's at 220° and 260° azimuth), but losses at higher frequencies were not so much in evidence. Indeed, at anterior contralateral angles of azimuth, (300° and 320°) pinna removal resulted in increases in gain of up to 9dB at frequencies above 11kHz. The likely cause of this is the loss of the "shadowing" effects of the recurved leading edge of the pinna. In comparison, the "shadowing" effects of the trailing edge of the pinna are relatively slight.

The pinna flange thus contributes substantially to the on-axis gain of the external ear over a wide frequency range, but also contributes to directional sensitivity. In particular, the leading edge of the pinna confers strong directional sensitivity in the anterior sector. This is probably one of the main sources of the large progressive changes in IID values that occur in the anterior sector.

5.7. Pinna Removal.

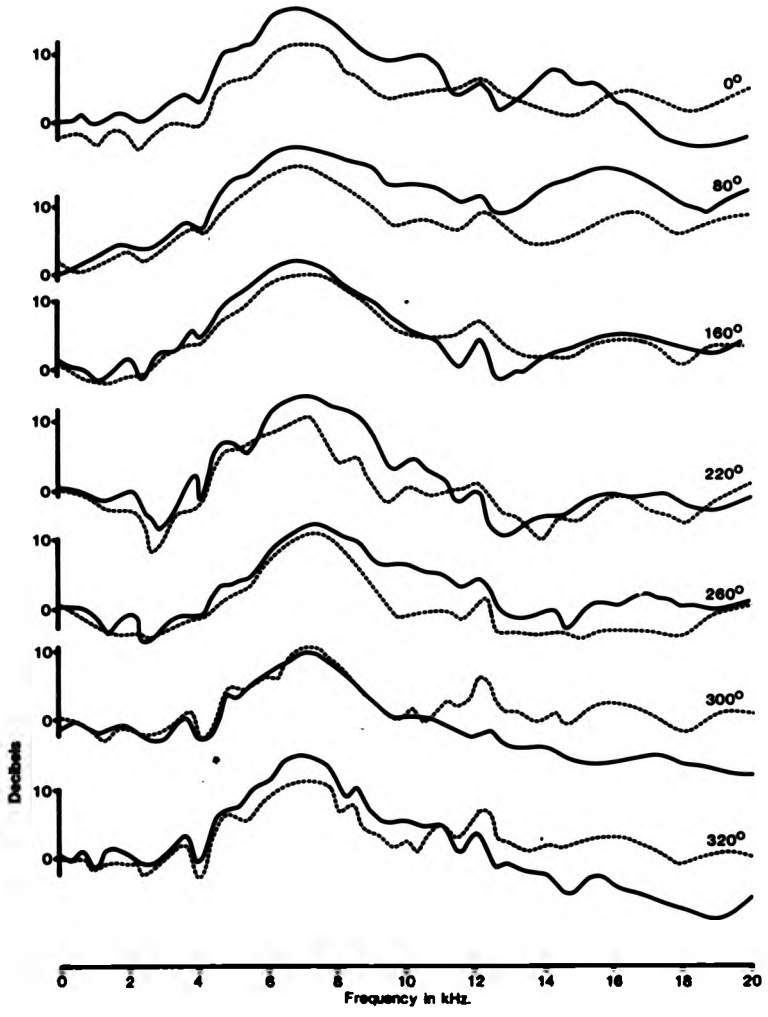
Following removal of the pinna flange, the pinna was

Figure 5.18: HRTF's from Rat Probe 2 at 0° elevation, (cadaver, right pinna facing 75° azimuth).

_____ pinna intact,

..... pinna flange removed.

Fig. 5.18


10
0
0°
80°
160°
220°
260°
300°
320°
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

removed, to leave the last 3-4mm of the concha opening flush onto the surface of the head. The results of this removal are shown for one animal for an ipsilateral and contralateral angle of azimuth in Fig.5.19. Pinna removal results in loss in gain at both 80° (Fig.5.19(a)) and 280° (Fig.5.19(b)) azimuth, although at the latter angle losses are restricted to the 5.5kHz-15.5kHz range because of the loss of the shadowing effects of the pinna. The pinna-removed HRTF at 80° azimuth shows gain of up to 7dB at various frequencies which may be accounted for by the effects of the head on the sound field. The HRTF at 280° azimuth approximates to free-field SPL levels over a wide frequency range. The null at 4.2kHz is not affected by pinna removal and is, therefore, presumably not caused by the effects of the pinna on the sound field. There is little indication from these studies of a resonance associated with the ear canal. Since the ear canal of the rats used in this study is about 7mm in length, with a mouth radius of 1.75mm, the expected fundamental resonance should be in the region of 10683Hz. No consistent HRTF gains occur at this frequency under pinna-removed conditions.

5.8. Other Experiments.

As part of the CM studies, either the tragal notch was blocked with vaseline, or the fossa was filled with plasticene and the effects of the modification monitored by recording the CM spectrum at selected angles of azimuth and

Figure 5.19: HRTF's from Rat Probe 4 at 0° elevation, (left pinna facing 60° azimuth):

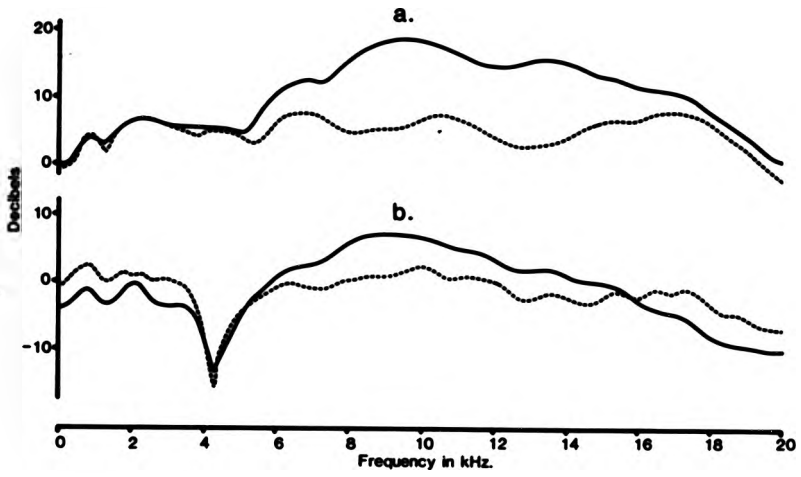
_____ pinna intact,

..... pinna removed.

(a) at 80° azimuth,

(b) at 280° azimuth.

Fig. 5.19


a.
b.
20
10
0
10
0
-10
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

elevation. The effects of the blocking of the tragal notch appear to have been negligible, while the blocking of the fossa appeared to reduce gain. Unfortunately, accurate quantification of these apparently relatively slight effects has not proved possible because of the instability of the CM over time. The results of these experiments are therefore not presented.

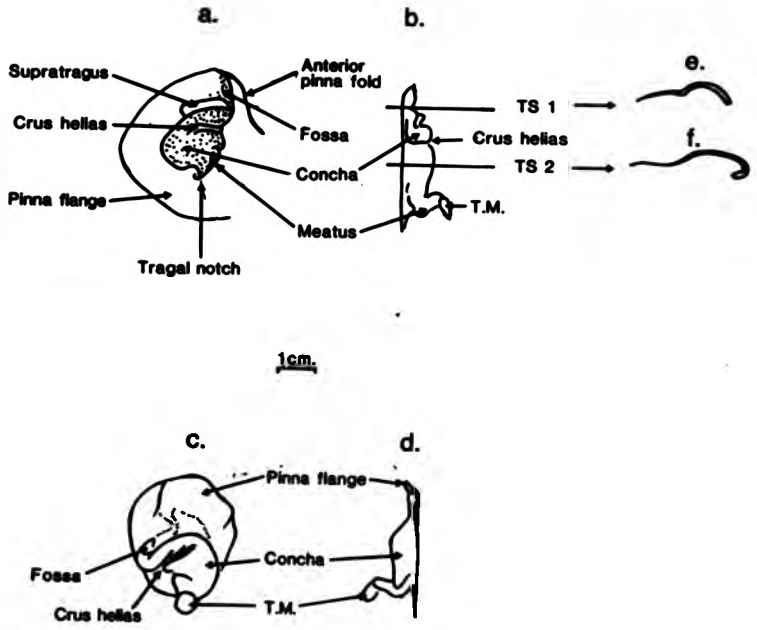
CHAPTER 6. RESULTS: THE GUINEA PIG.

6.1. Anatomy of the External Ear.

The sizes of the pinnae of experimental subjects were monitored by measuring the distance between the top margin of the pinna and the base of the tragal notch. These measures ranged from 2.7cm to 2.9cm. Endocasts of the external ears were made by introducing Silastic E under vacuum (760mm Hg for 2hrs) with a small hole bored in the base of the ear canal. Figure 6.1 shows drawings of the external ear of which (a) is an external view, (b), (c) and (d) are drawings of an endocast, and (e) and (f) are drawings from sections cut from the pinna of a cadaver. The leading edge of the pinna is recurved while the trailing edge is practically flat (Fig.6.1(e) and (f)). Associated with the leading edge is a clearly demarcated cavity which is here termed the fossa. The fossa is largely separated from the concha by a ridge, the supratragus, but the 2 cavities are confluent anteriorly. A similar arrangement obtains for most human ears. The concha is subdivided by a second ridge, (here termed the crus helias). There is a shallow tragal notch (Fig.6.1(a)). The ear canal enters the concha approximately at right angles to the plane of the pinna mouth (Fig.6.1 (b) and (d), and turns through about 90° to terminate in the cavity housing the TM. Measurements from an external ear of pinna length 2.7cm were as follows: ear canal entrance to TM, 6mms; ear canal entrance to end of cavity housing the TM, 10mms; ear canal diameter at entry point to concha, 3.75cm; ear canal diameter at entry

Figure 6.1: Drawings of the right external ear of a guinea pig. (a) external view of pinna, (b), (c) and (d) anterior, contralateral and posterior views of an endocast (GPC, pinna length 2.7cm).
(e) and (f) horizontal sections through the pinna at the levels indicated in (b).

Fig. 6.1


a.
b.
e.
f.
Supratragus
Anterior pinna fold
Crus helias
Fossa
Concha
Pinna flange
Meatus
Tragal notch
TS 1
TS 2
Crus helias
T.M.
1cm.
c.
d.
Pinna flange
Concha
Fossa
Crus helias
T.M.

point to cavity housing the TM, 2.8cm; diameter of TM, 7mm; maximum concha depth (pinna mouth to medial wall of concha) 7.5mm.

6.2. Directional Characteristics of the External Ear.

Azimuthal dependence functions were obtained from 3 cadavers by means of probe implant in the wall of the meatus (GPA and GPB) or by probe implant into the tympanic cavity (GPD). Pure tones at selected frequencies were monitored for every 20° azimuth at 0° elevation. A typical set of azimuthal dependence functions is shown in Fig.6.2. Up to 10kHz, the main lobes of the functions are orientated to approximately 60°. Covert maxima, reminiscent of the "bright spot" of human azimuthal dependence functions, occur between 210° and 240° azimuth. At 16kHz and above, the main lobes are less broad and are orientated more posteriorly to between 78° and 100° azimuth. -3dB acceptance angles calculated from the 3 sets of azimuthal dependence functions are shown plotted as functions of frequency in Fig.6.3. Above 6kHz the functions drop below 90°, thence falling steadily to between 40° and 44° azimuth.

6.3. Head Related Transfer Functions.

HRTF's were obtained from 3 guinea pigs where the probe was implanted through the side wall of the ear canal near its base, and from 3 guinea pigs, where the probe was

Figure 6.2: Azimuthal dependence functions at 0° elevation obtained using pure tones. (From GPA, probe implant in meatus, left pinna facing 55° azimuth.)

Fig. 6.2

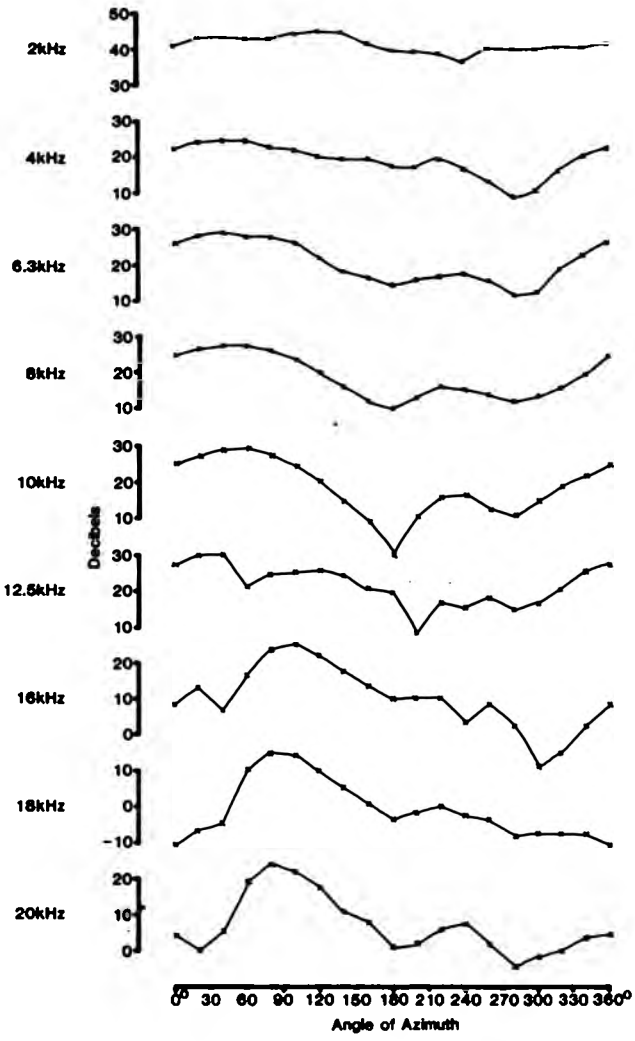
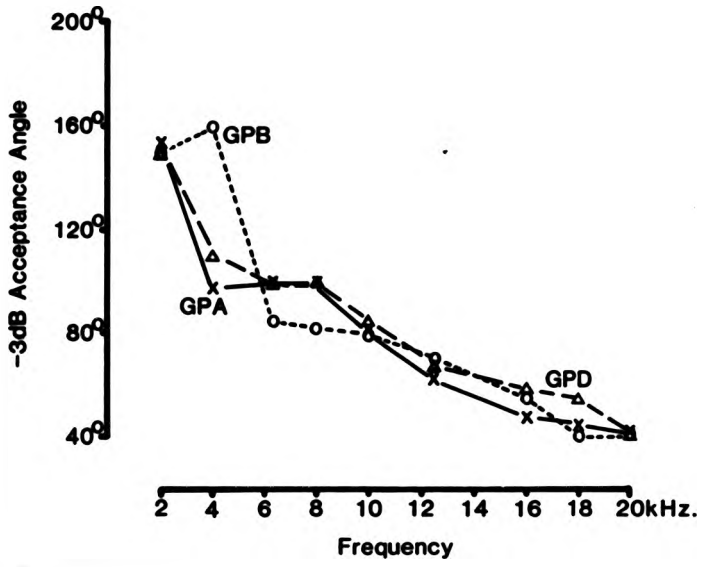

2kHz
4kHz
6.3kHz
8kHz
10kHz
12.5kHz
16kHz
18kHz
20kHz
Decibels
0° 30 60 90 120 150 180 210 240 270 300 330 360°
Angle of Azimuth

Figure 6.3: -3dB acceptance angles at 0° elevation for 3 guinea pigs plotted as functions of frequency.

Fig. 6.3


200°
160°
120°
80°
40°
-3dB Acceptance Angle
GPB
GPA
GPD
2
4
6
8
10
12
14
16
18
20kHz.
Frequency

implanted through the ventrolateral wall of the tympanic bulla into the cavity housing the TM (the tympanic cavity).

A typical set of HRTF's at 0° elevation from an ear canal implant study is shown in Fig.6.4 (GPA, pinna length 2.9cm). A consistent peak of up to 18dB occurs at 3kHz throughout this set of HRTF's. Maximum gain (up to 17dB) in the 6kHz to 14kHz range occurs at 40° azimuth (Fig.6.4(a)) but overall maximum gain (26-28dB) occurs in the 15kHz to 18kHz range at 80° and 100° azimuth (Fig.6.4(b)). Gain at contralateral angles is, by comparison, reduced throughout most of the frequency range (Fig.6.4(c)). Minima occur consistently in the 4.5kHz to 5.0kHz region and occasionally at other frequencies (e.g. 9.8kHz at 180° azimuth). Changes in gain with changes in angle of azimuth show clearest progression in the posterolateral sector HRTF's (Fig.6.4(b)).

HRTF's at different angles of elevation (Fig.6.5) show progressive up-frequency shifts in minima in the 11.0kHz to 13.5kHz range with increasing elevation. There are also progressive increases in gain in the 10kHz to 12kHz range.

A set of HRTF's from a tympanic cavity probe implant study (GPC, pinna length 2.7cm) is shown in Fig.6.6. A consistent peak of up to 10dB occurs at between 2.0kHz and 2.4kHz. Maximum gain (15.5dB) occurs in the 14kHz to 15kHz region at 100° azimuth (Fig.6.6(b)), but gain in the 4kHz to 10kHz range is largest (9dB) at 40° azimuth (Fig.6.6(a)). Minima occur at about 3kHz and in the 11kHz region. At higher frequencies (14kHz and above), the levels

Figure 6.4: A series of HRTF's at 0° elevation:
(a) anterior-ipsilateral sector,
(b) posterior-ipsilateral sector,
(c) sample contralateral spectra. (From GPA, probe implant in meatus, left pinna facing 55° azimuth.)

Figure 6.5: A series of HRTF's at 80° azimuth for various elevations. (From GPA, probe implant in meatus, left pinna facing 55° azimuth.)

Fig. 6.4

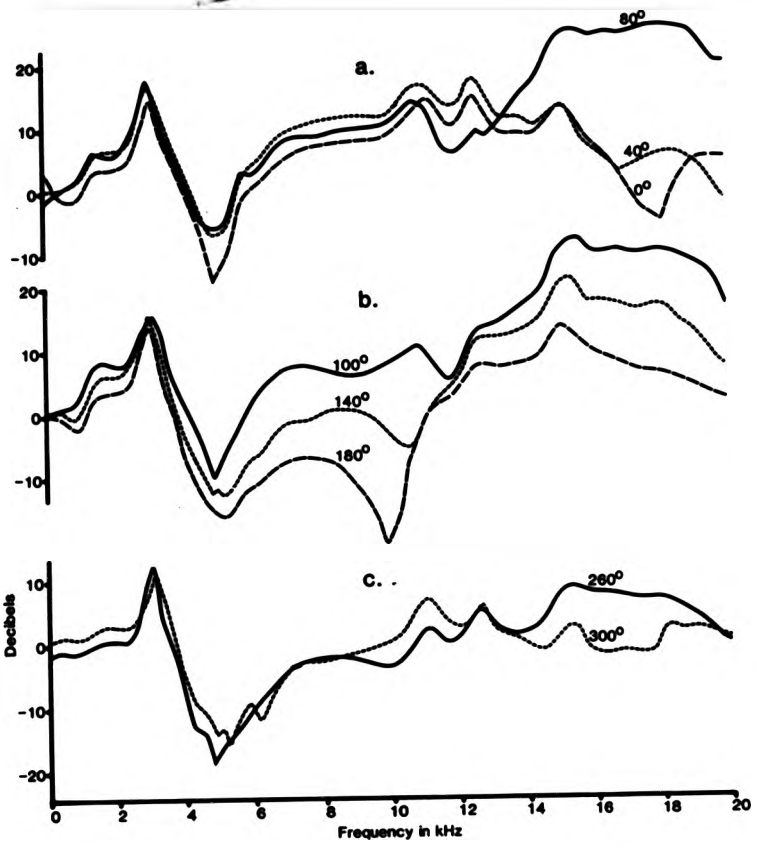

a.
b.
c.
80°
40°
0°
100°
140°
180°
260°
300°
Decibels
Frequency in kHz

Fig. 6.5

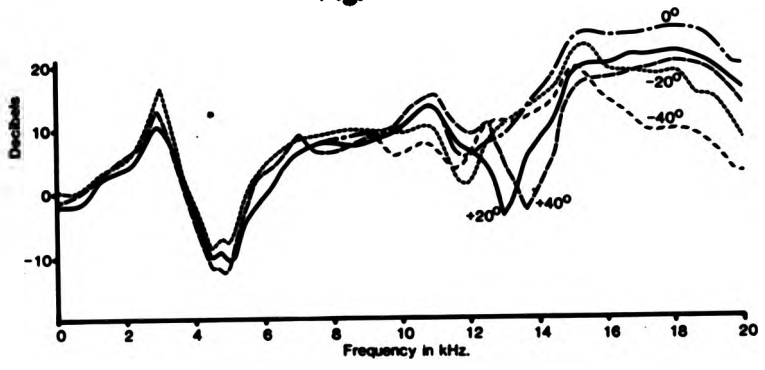
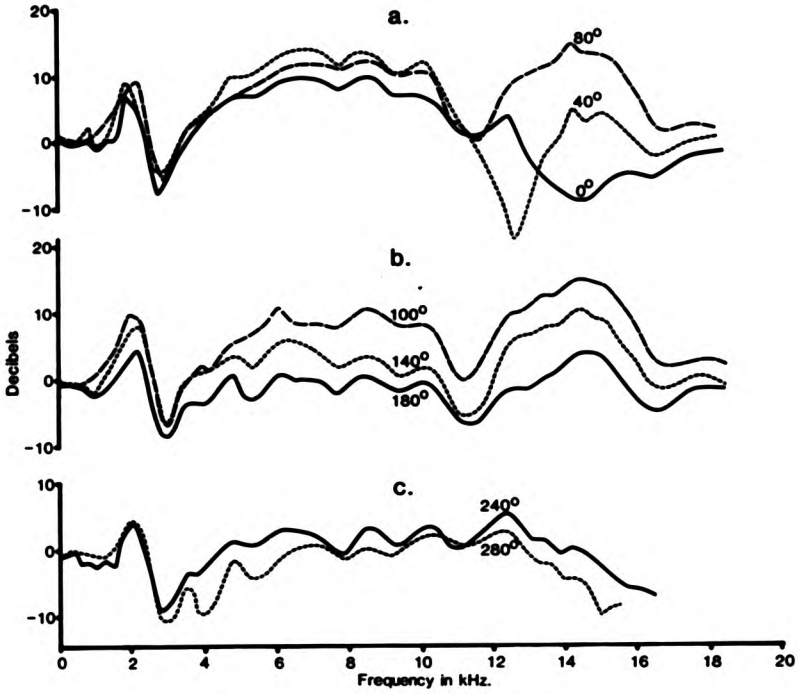

0°
-20°
-40°
+20°
+40°
Decibels
Frequency in kHz.

Figure 6.6: A series of HRTF's at 0° elevation:
(a) anterior-ipsilateral sector,
(b) posterior-ipsilateral sector,
(c) sample contralateral spectra. (From GPC, probe implant in tympanic cavity, left pinna facing 50° azimuth).

Fig. 6.6


a.
80°
40°
0°
b.
100°
140°
180°
c.
240°
280°
Decibels
20
10
0
-10
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

of gain shown by the HRTF's obtained from GPC are about 5dB or more below those obtained from GPA. This difference was found to occur between all the ear canal and tympanic cavity implant studies.

Three elevation HRTF series for GPC are shown in Fig.6.7. At 80° azimuth (Fig.6.7(a)), there are progressive shifts in minima and increases in gain with increasing elevation in the 10kHz to 13kHz range. This trend occurs at all ipsilateral angles of azimuth, but sharp minima are not always present in the HRTF's in this frequency range. At 0° (Fig.6.7(c)) and also at 40° azimuth, minima tend to occur at higher frequencies. At contralateral angles of azimuth (Fig.6.7(b)), progressive increases in gain also occur with increasing elevation, but the occurrence of nulls is erratic.

Checks on the stability of HRTF's in guinea pig preparations, revealed a progressive loss in gain with time. HRTF's obtained at various times after sacrifice are shown in Fig.6.8. The loss in gain (5dB) in the peak at 2kHz was particularly evident, but losses (of up to 4.5dB) occurred throughout the frequency range. Increases in gain occurred with time in the 3kHz region (Fig.6.8(b)). In experiments where part or all of the guinea pig pinna was removed (described below in 6.7 and 6.8) the changes in HRTF's with time have to be taken into account.

6.4. Cochlear Microphonic Recordings

CM's were recorded from 8 guinea pigs using the

Figure 6.7: HRTF's at various elevations at;
(a) 80° azimuth,
(b) 280° azimuth,
(c) 0° azimuth. (From GPC, probe implant in tympanic cavity, left pinna facing 50° azimuth.)

Figure 6.8: HRTF's at 0° elevation at various times after death:
(a) 0° azimuth,
(b) 80° azimuth. (From GPC, probe implant in tympanic cavity, left pinna facing 50° azimuth.)

Fig. 6.7

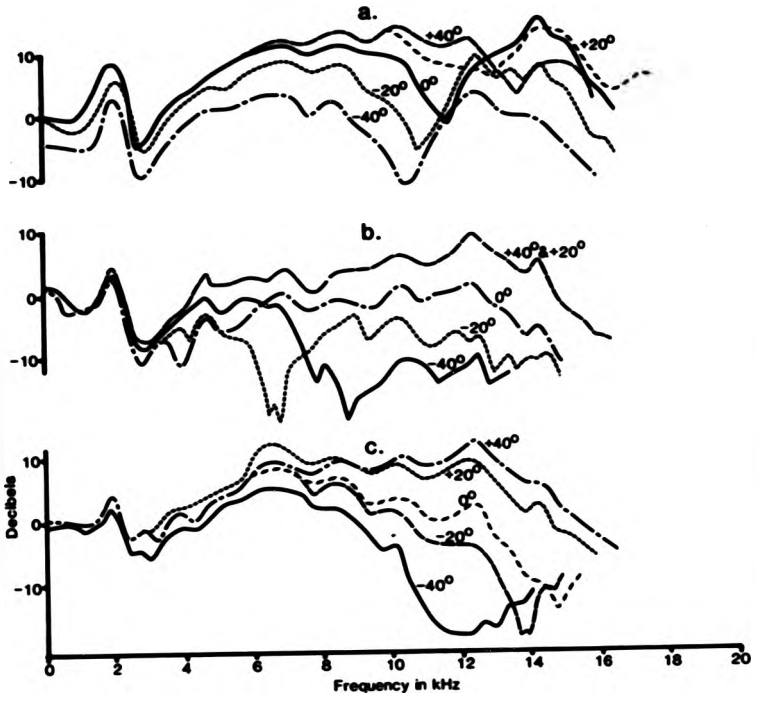
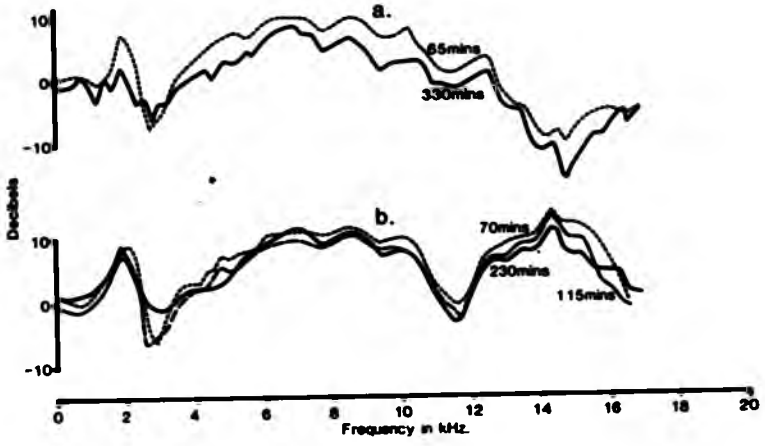

a.
b.
c.
+40°
+20°
0°
-20°
-40°
10
0
-10
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz

Fig. 6.8


a.
65mins
330mins
b.
70mins
230mins
115mins
10
0
-10
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

techniques described in Chapter 2. Maximum CM's were typically between 130uV and 135uV but in one preparation (GP2) the maximum was 101uV. The relationship between CM amplitude and signal SPL was determined for each preparation using pure tones at 6 frequencies. The CM amplitude : signal SPL ratios ranged from 8.87 to 0.93. Broad-band sound was not used to determine the relationship between CM amplitude and signal SPL. Comparisons of CM and probe implant IID spectra indicate that the CM amplitude : broad-band signal SPL is in the region of 0.7. It is not, however, possible to quantify the CM spectra obtained from guinea pigs with any precision. They do, however, provide qualitative information which, in general, supports the findings of the probe implant studies. Fig. 6.9 shows sample spectra at 0° elevation from a typical preparation (GP6). Clear separation of the spectra in the anterior-ipsilateral sector occurs only between about 17kHz and 23kHz (Fig.6.9(a)), whereas separation of posterior-ipsilateral spectra occurs over this frequency range and in the 8kHz to 9kHz region (Fig.6.9(b)). This was also found to be the case in the probe implant studies (see Fig.6.4).

In only one CM preparation (GP8) was a distinct peak in the 2kHz to 3kHz region discernible, and in this respect the CM and probe implant data are not in agreement. Sample spectra from GP8 are shown in Fig.6.10. There is a distinct peak at 3kHz in all the spectra obtained from this preparation. Apart from this, the spectra are similar to those obtained from other CM studies, and show the stronger

Figure 6.9: A series of CM spectra at 0° elevation:

(a) anterior-ipsilateral sector,

(b) posterior-ipsilateral sector,

(c) sample contralateral spectra. (From GP6, left pinna facing 45° azimuth.)

Fig. 6.9

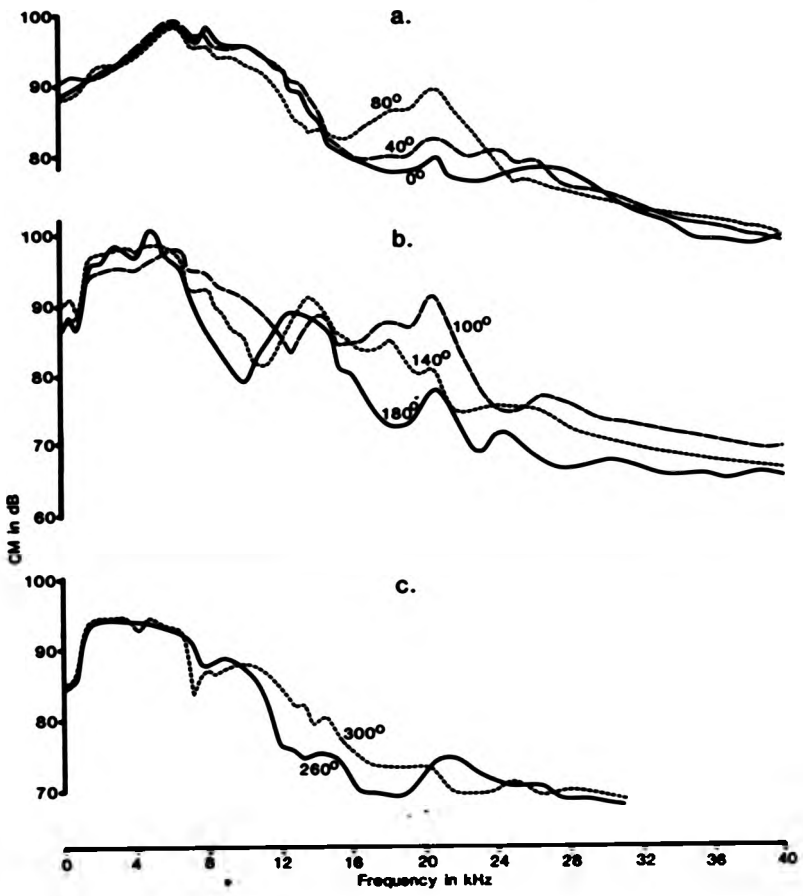

a.
b.
c.
100
90
80
70
60
80°
40°
0°
100°
140°
180°
300°
260°
CM in dB
0
4
8
12
16
20
24
28
32
36
40
Frequency in kHz

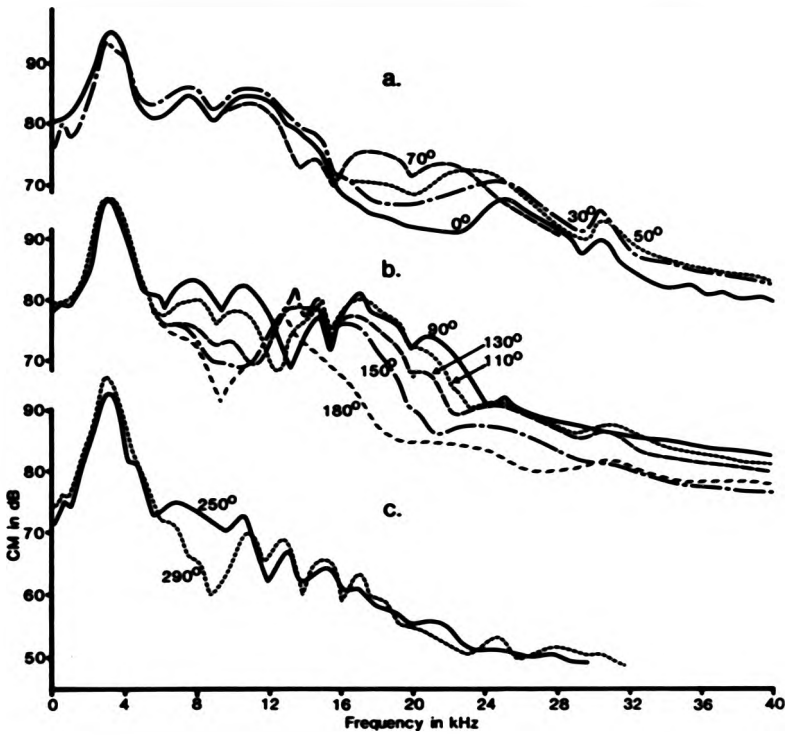
Figure 6.10: A series of CM spectra at 0° elevation;

(a) anterior-ipsilateral sector,

(b) posterior-ipsilateral sector,

(c) sample contralateral spectra. (From GP8, left pinna facing 45° azimuth.)

Fig. 6.10


a.
b.
c.
70°
0°
30°
50°
90°
130°
110°
150°
180°
250°
290°
CM in dB
Frequency in kHz
90
80
70
60
50
0
4
8
12
16
20
24
28
32
36
40

separation of spectra over a larger frequency range in the posterior-ipsilateral sector.

Like the probe implant HRTF's, CM spectra show progressive increases in the 12kHz to 16kHz range with increasing elevation. A series of CM spectra at 60° azimuth has been plotted over the 50Hz to 20kHz range in order to demonstrate this point (Fig.6.11). CM spectra at 80° and 280° azimuth from the same preparation (GP6) are presented in Fig.6.12 plotted over the 100Hz to 40kHz range. The progressive changes in the spectra with increasing elevation appear to be confined to the 12kHz to 16kHz range. Furthermore, they are not clearly shown in contralateral spectra (Fig.6.12(b)). Comparison of Figs.6.11 and 6.12(a) will show that sharp minima do not occur at all angles of incidence; there are no sharp minima in the spectra at 60° azimuth (Fig 6.11) and they occur sporadically at various elevations at other angles of azimuth.

6.5. Interaural Intensity Differences.

IID's at 0° elevation calculated from an azimuthal dependence study using pure tones are shown plotted as functions of frequency in Fig.6.13. The largest IID's tend to occur in the 16kHz to 18kHz, the function at 80° azimuth showing the largest values at most frequencies (e.g. 28dB at 20kHz). IID spectra obtained from CM studies show general agreement with those obtained from probe implants but, because of the extended frequency range available with

Figure 6.11: CM spectra at 60° azimuth for various elevations (50Hz-20kHz). (From GP6, left pinna facing 45° azimuth.)

Figure 6.12: CM spectra at various elevations:
(a) 80° azimuth,
(b) 280° azimuth (100Hz-40kHz). (From GP6, left pinna facing 45° azimuth.)

Fig. 6.11

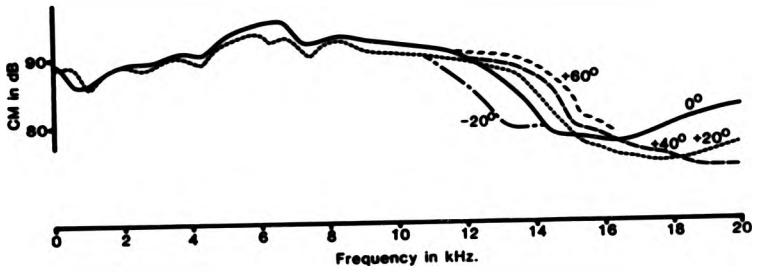
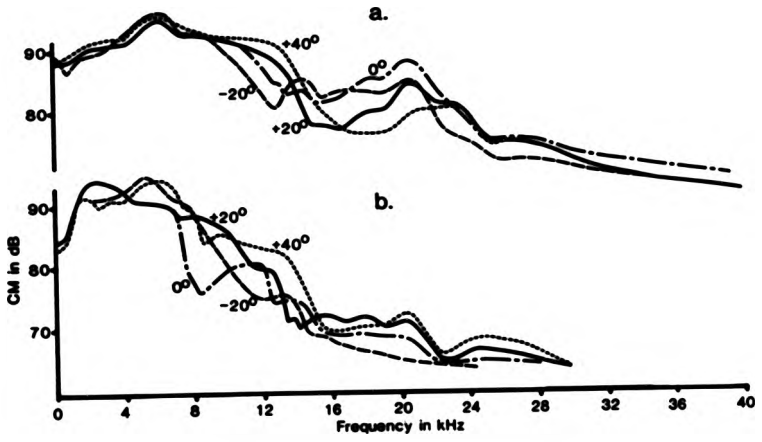


Fig. 6.12



CM recordings, it is clear that there are large IID's above 20kHz (Fig.6.14). The apparent decrease in IID's above 20kHz is probably artifactual owing to the fact that CM's at contralateral angles of azimuth approach noise levels above 20kHz (see Figs.6.9(c) and 6.10(c)).

IID spectrum features such as maxima and minima show progressive up-frequency shifts with increasing elevation. This was found to occur in all the CM studies and in the probe study where IID's were obtained. Fig.6.15 shows a series of IID spectra at 80° azimuth for various elevations obtained during a probe study (GPA). The minima in the 12kHz-14kHz region show progressive up-frequency shifts with increasing elevation. The peak at 8.5kHz in the -20° elevation spectrum is probably the result of head and platform "shadow". Fig.6.16 shows a series of CM IID spectra where it is clear that accompanying the up-frequency shift of the minima is a progressive up-frequency shift in the maxima in (for this animal) the 20kHz to 24kHz region.

IID's at various frequencies plotted as functions of azimuth at 0° elevation (from a pure tone study, probe implant GPA) are shown in Fig.6.17. IID's rise steadily in the anterior sector at lower frequencies (4kHz, 8kHz) but are non-monotonic at higher frequencies (16kHz, 20kHz). At 16kHz, the mean rate of change of IID with angle of azimuth in the anterior sector (0° to 60° azimuth) is 0.4dB per 1° azimuth. Posterior sector IID functions are non-monotonic at all frequencies tested.

Figure 6.13: IID's at 0° elevation plotted as functions of frequency:
(a) anterior sector.
(b) posterior sector.
(From a pure tone study on GPA, probe implant in meatus, left pinna facing 55° azimuth.)

Figure 6.14: CM IID spectra at 0° elevation:
(a) anterior sector.
(b) posterior sector.
(From GP6, left pinna facing 45° azimuth.)

Fig. 6.13

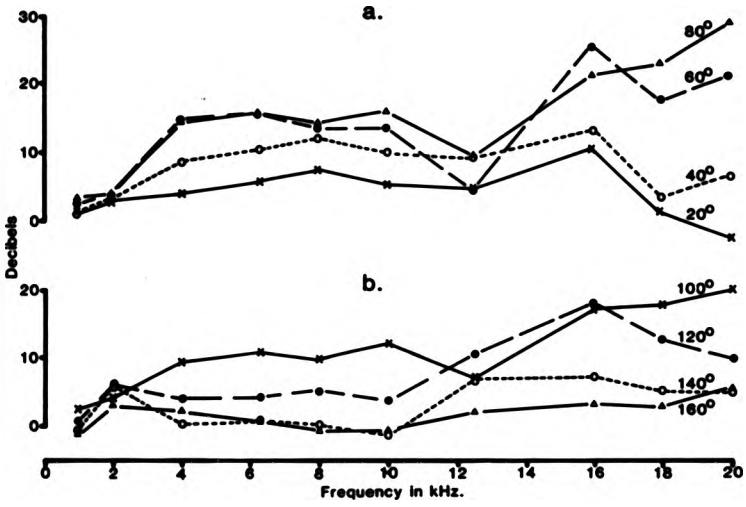


Fig. 6.14

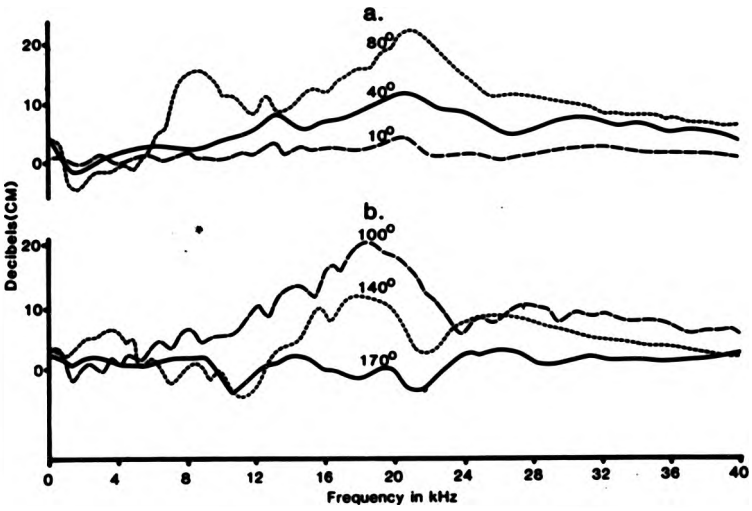


Figure 6.15: IID spectra at 80° azimuth for various elevations. (From GPA, probe implant in meatus, left pinna facing 55° azimuth.)

Fig. 6.15

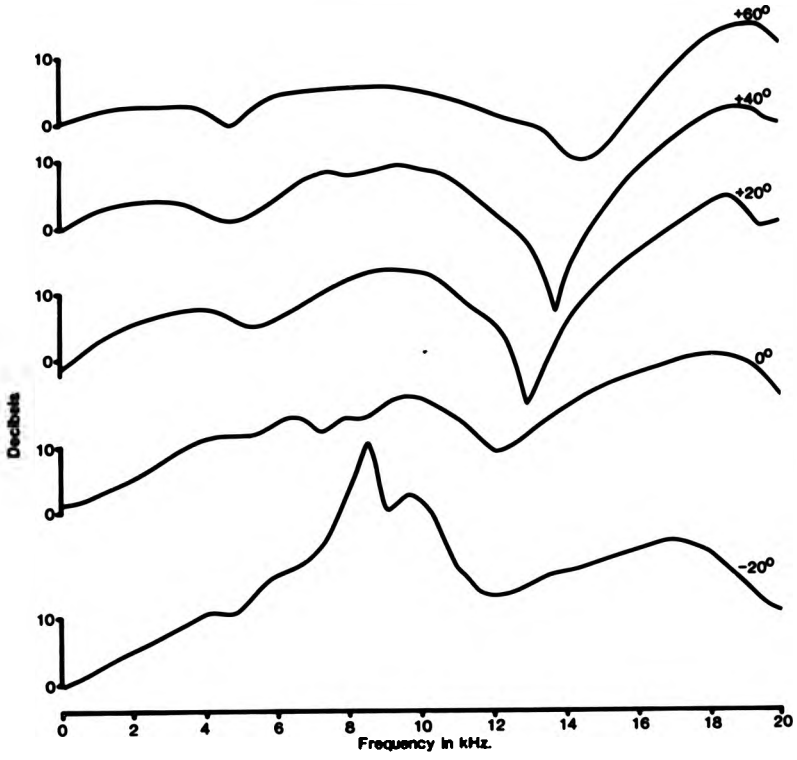

+60°
+40°
+20°
0°
-20°
10
0
DecBels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 6.16: CM IID spectra at 80° azimuth for various elevations. (From GP6, left pinna facing 45° azimuth.)

Figure 6.17: IID's at 0° elevation plotted as functions of angle of azimuth. (From GPA, probe implant in meatus, left pinna facing 55° azimuth.)

Fig. 6.16

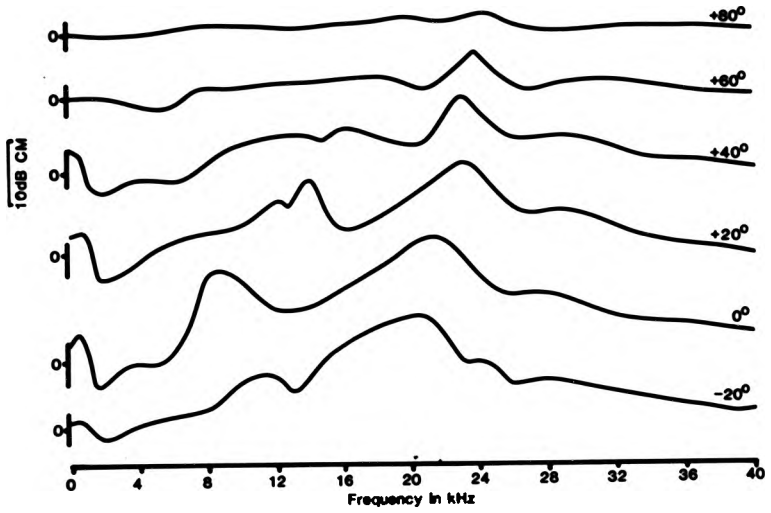
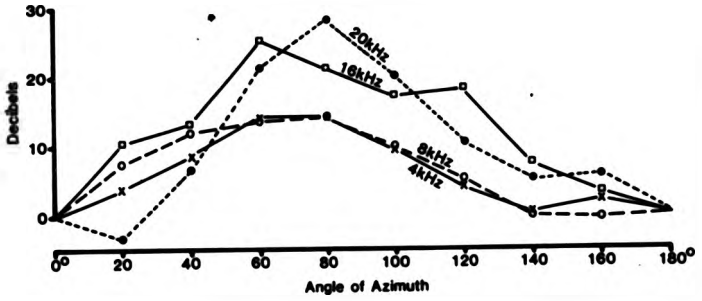


Fig. 6.17



6.6. Blocking the Fossa.

The effects of blocking the fossa were investigated during the course of 3 probe implant studies. Blocking was effected by placing a 7mm diameter ball of plasticene in the fossa. No discernible change in pinna orientation occurred during the blocking. The major effect of the block was to cause a down-frequency shift in the anterior-ipsilateral HRTF minima in the 14kHz to 15kHz region. A series of HRTF spectra at 0° elevation is shown in Fig.6.18. The small changes in gain that occur throughout the frequency range are the result of the instability of the preparation. The shift in the minimum in the 0° azimuth spectrum is the most obvious effect of fossa blocking. Investigation of the effects of blocking the fossa was made for various elevations for a range of angles of azimuth. The effects are confined to the anterior-ipsilateral HRTF's and are strongest at -20° and 0° elevation (see Fig.6.19). The likely cause of the HRTF minima in the 10kHz to 16kHz region is destructive interference. This is discussed in chapter 8.

6.7. Removal of the Anterior Pinna Flange.

The anterior pinna fold and the part of the pinna flange immediately posterior to it were cut away with a pair of scissors during the course of 3 probe implant studies (see Fig.6.20). The removal resulted in increase in gain of up to 20dB in HRTF's at 0° and 40° azimuth (0° elevation) in the 12kHz to 17.5kHz region but losses in gain at 80° and

Figure 6.18: HRTF's at 0° elevation;

_____ pinna intact,

..... fossa blocked.

(From GPC, probe implant in tympanic cavity, left pinna facing 50° azimuth.)

Fig. 6.18

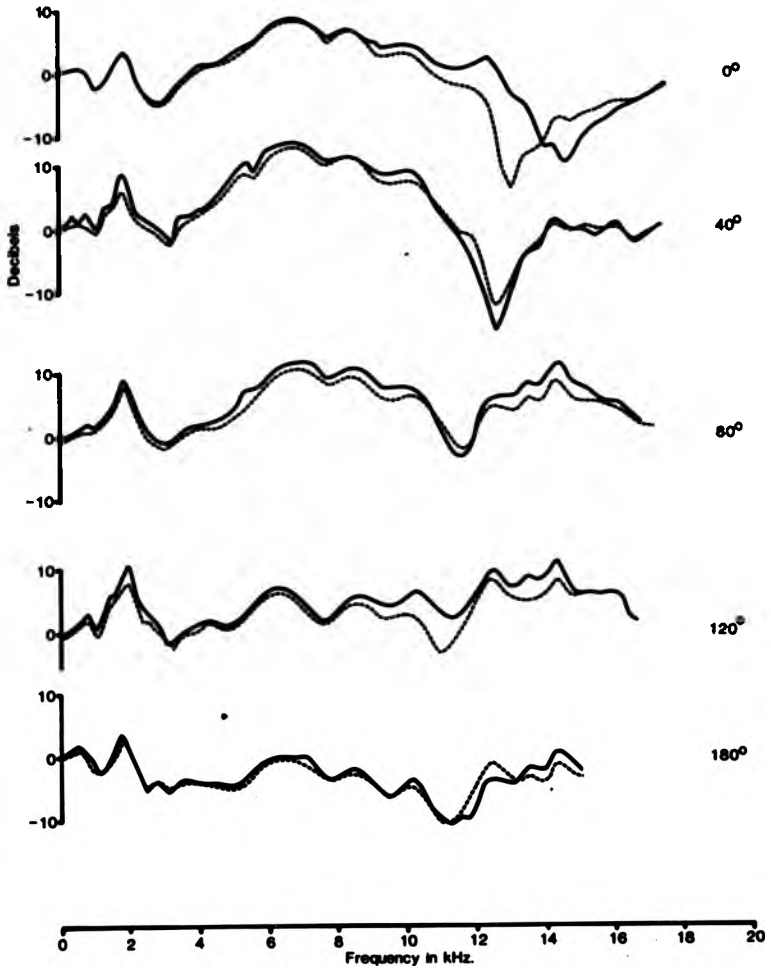

10
0
-10
Decibels
0°
40°
80°
120°
180°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 6.19: HRTF's at 0° azimuth for various elevations:

_____ pinna intact,

..... fossa blocked.

(From GPC, probe implant in tympanic cavity left pinna facing 50° azimuth.)

Fig. 6.19

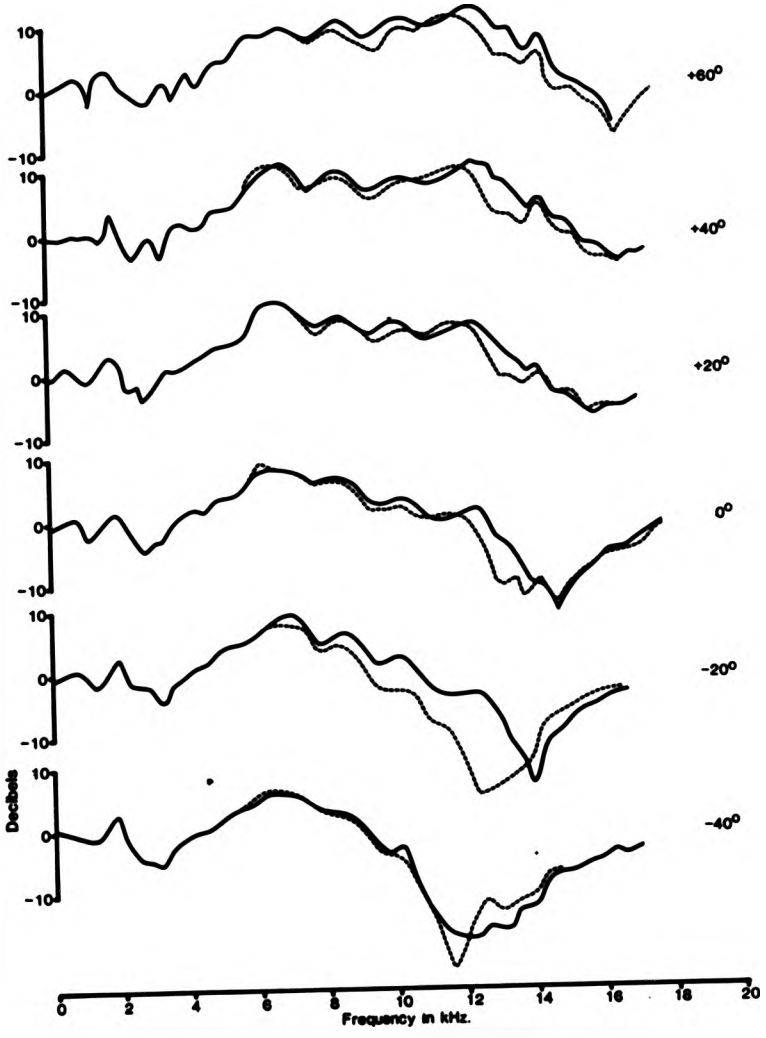

10
0
-10
+60°
+40°
+20°
0°
-20°
-40°
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Figure 6.20: HRTF's at 0° elevation:

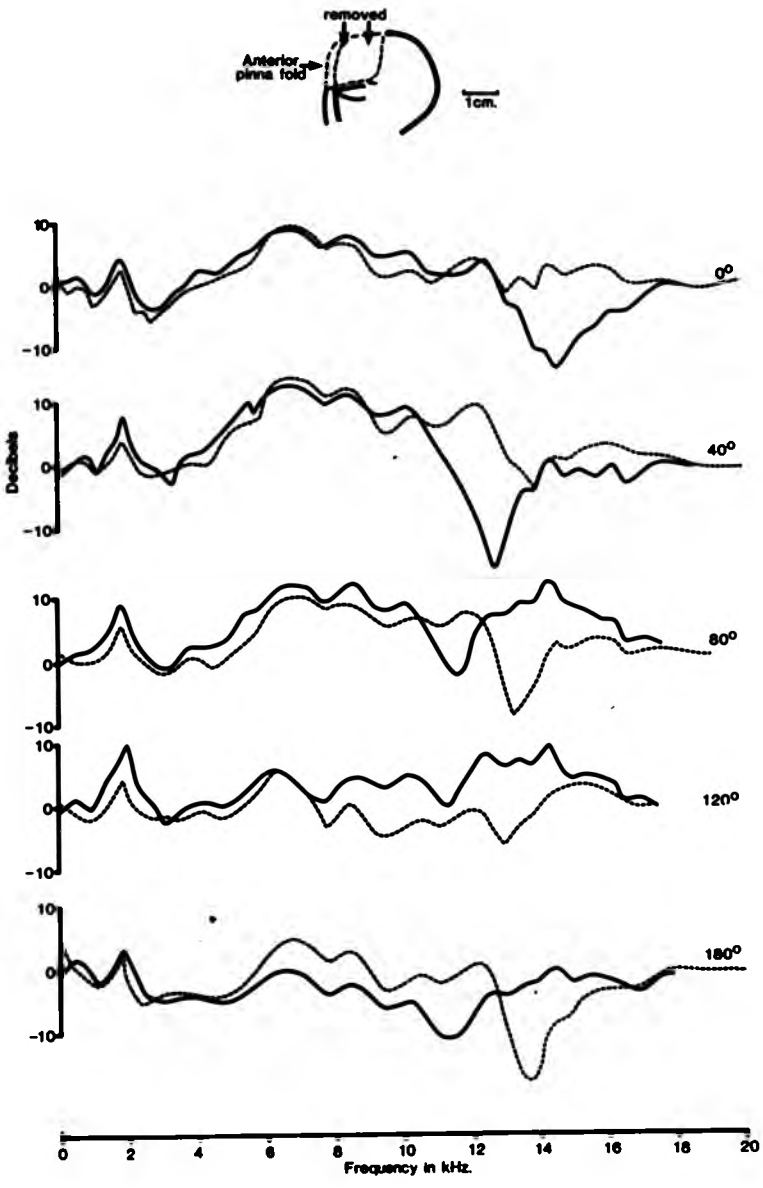
_____ pinna intact,

..... anterior pinna flange removed.

The insert shows the amount of pinna flange removed.

(From GPC, probe implant in tympanic cavity, left pinna facing 50° azimuth.)

Fig. 6.20


removed
Anterior pinna fold
1cm.
10
0
-10
0°
40°
80°
120°
180°
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

120° azimuth. The losses at 120° azimuth extended over the 8kHz to 14kHz range and were up to 12.5dB. These changes are readily interpreted as the results of loss of the "shadow" of the anterior pinna fold in the anterior sector and loss of reflections from the fold into the concha when the sound source was lateral in position. However, at 180° azimuth, there is an increase in gain over the 6kHz to 12kHz range (up to 8.5dB). This is surprising. Instability of the preparation may be contributory to this (see below), but the large size of the effect suggests other, unknown causes. There is a loss in gain in the 180° azimuth HRTF between 13kHz and 16kHz (up to 14.5dB). This is similar to the losses shown in other ipsilateral spectra, and indicates that the anterior pinna fold serves to increase gain at higher frequencies from lateral and posterior angles of azimuth.

6.8. Removal of the pinna flange.

The whole of the pinna flange was removed with a pair of scissors during the course of 3 probe implant studies. Fig.6.21 shows a series of HRTF's at 0° azimuth from one such experiment. The main effects of the removal appear to be generally a loss of gain for ipsilateral HRTF's and increases or little change in gain contralaterally (HRTF's at 280° and 320° azimuth) The 0° azimuth HRTF, however, shows increase in gain in the 14kHz to 16kHz region whereas there are decreases in gain at these frequencies at 180°, 200° and 240° azimuth. Loss of anterior pinna fold "shadow"

Figure 6.21: HRTF's at 0° elevation:

_____ pinna intact,

..... pinna flange removed.

(From GPC, probe implant in tympanic cavity, left pinna facing 50° azimuth.)

Fig. 6.21

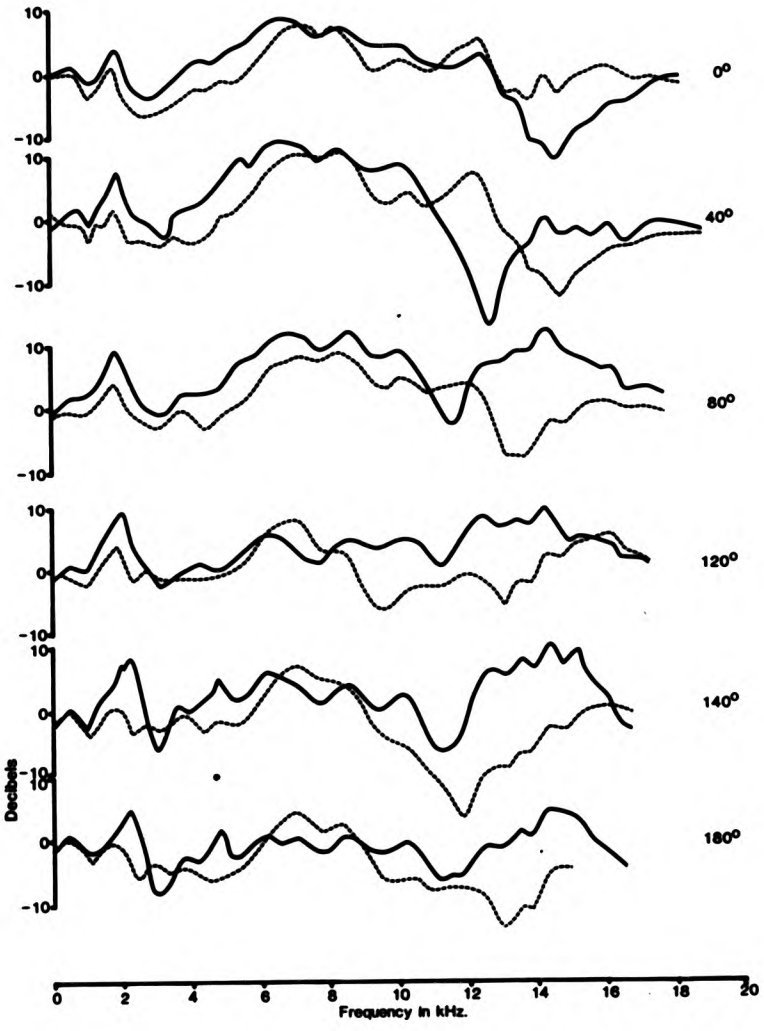
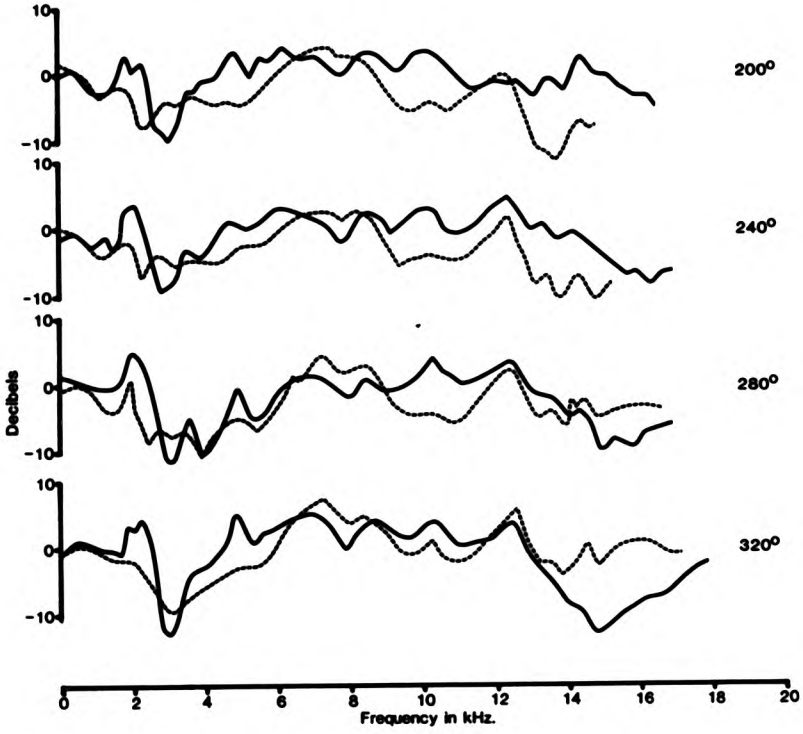

10
0
-10
0°
40°
80°
120°
140°
180°
Decibels
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

Fig. 6.21 cont'd.



and reflection respectively are likely causes of these changes. The pinna flange removal appears to have similar effects to anterior pinna flange removal at ipsilateral angles of azimuth. The major differences between the two sets of spectra is the loss of gain in the 4kHz to 8kHz region accompanying removal of the whole of the pinna flange. The posterior part of the pinna flange thus appears to contribute gain in this frequency region. These effects are difficult to quantify, however, because of the instability of the preparations; there is a general increase in gain in the 8kHz region as a consequence of changes in the TM (see below). This confounds the effects of pinna flange removal in this frequency region.

6.9. Removal of the pinna.

The whole of the pinna was removed during the course of 3 probe implant studies. The base of the concha was severed with a scalpel to leave the ear canal opening flush with the surface of the head. HRTF's from one preparation (GPC) at 3 angles of incidence are shown in Fig.6.22. Large losses in gain result (up to 18dB) throughout most of the frequency range at all angles of incidence. The peak in each HRTF at 2kHz does not, however, appear to be affected by pinna removal. The changes in gain at 2kHz are the result of the instability of the preparation. Above 2kHz, it is clear that HRTF gain is a consequence of the action of the pinna on the sound field. Contralateral pinna-removed functions are typically in the region of 10dB below

the ipsilateral functions over an extensive frequency range (compare Fig.6.22(a) and (c)). This suggests head obstacle effects on the sound field.

6.10. Puncturing the Tympanic Membrane.

Following pinna removal, the TM was punctured by inserting a stiff wire into the open end of the ear canal. This was done at the end of 3 probe implant studies with the same result; puncturing the TM resulted in an increase in gain in the peak in the 2kHz to 3kHz region (up to 6.5dB), and an increase in gain in the HRTF (up to 4dB) throughout most of the frequency range above the low frequency peak (see Fig.6.23). Progressive losses in gain in the low frequency HRTF peak, and changes in gain, particularly in the 8kHz region (see Fig.6.8) occur during the course of each probe implant study on the guinea pig. Since puncturing the TM restores the low frequency peak to the same levels as that of a freshly killed guinea pig, it seems likely that changes in the acoustic impedance of the TM are the causes of the instability of the HRTF's over time. The low frequency HRTF peak is, presumably, associated with the ear canal but, since puncturing the TM restores the peak to its early level (accurate comparisons are not possible because of the removal of the pinna), the middle ear cavity may also be involved in the generation of the peak.

Figure 6.22: HRTF's at 0° elevation;

_____ pinna intact,

..... pinna removed.

(a) at 80° azimuth,

(b) at 180° azimuth,

(c) at 280° azimuth.

(From GPC, probe implant in tympanic cavity, left pinna facing 50° azimuth.)

Figure 6.23: HRTF's at 180° azimuth, 0° elevation with pinna removed:

_____ TM intact,

..... TM punctured.

(From GPC, probe implant in tympanic cavity, left pinna facing 50° azimuth.)

Fig. 6.22

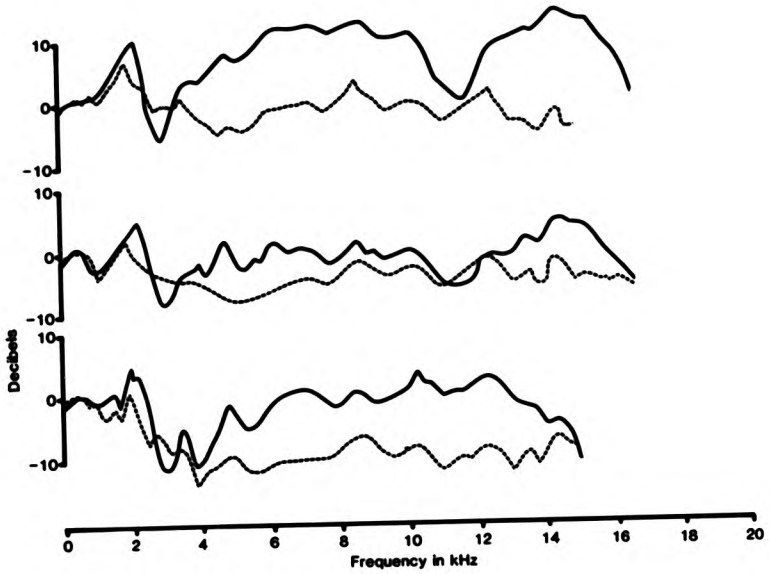
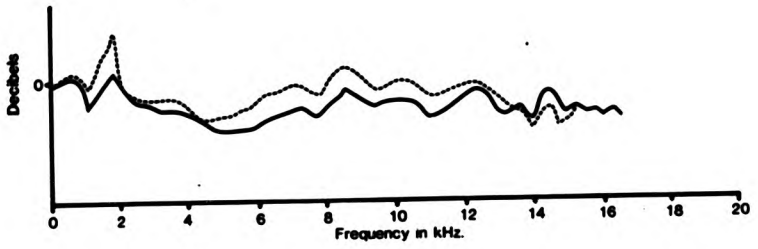


Fig. 6.23



CHAPTER 7. RESULTS: INTERAURAL TIME DIFFERENCES.

7.1. Introduction.

Changes in phase angle with changes in the angle of incident sound were monitored during the course of both CM and biophysical investigations. The equipment used is described in chapter 2. The phase angle at the ear was always measured relative to the signal at source (the pure tone generator), and measurements were made for every 10° or 20° azimuth at 0° elevation for pure tones at various frequencies between 1kHz and 8kHz. In 3 of the rabbit biophysical studies, phase angle measurements were also made at various elevations.

Interaural phase differences (IPD's) were calculated by subtracting the phase angles at ipsilateral angles of azimuth from the phase angles at the mirror image contralateral angles of azimuth.

Phase angles obtained from CM studies proved, in the main, to change erratically as the angle of incidence of the sound changed. The causes of this are not known. The IPD's plotted as functions of azimuth, which are presented below, are therefore all based on data obtained during biophysical investigations.

7.2. The Rabbit.

IPD's at 0° elevation plotted as functions of azimuth at 3 frequencies are shown in Fig.7.1. The recorded pinna of this preparation (MG16, a cadaver with a microphone

implanted in the tympanic bulla) was facing 38° azimuth. IPD values increase progressively with increasing frequency at most angles of azimuth and the maximum IPD's occur posterior to the interaural axis (90°). The gradient of the functions is greater in the posterolateral sector. The 2kHz and 3kHz functions are non-monotonic between 0° and 50° azimuth. This was not the case for all the rabbits investigated, 2 preparations showing monotonic increases in IPD's in the anterolateral sector at all frequencies employed.

Reorientating the recorded pinna to face posterolaterally resulted in IPD functions with greater gradients in the anterolateral sector (see Fig.7.2). This result was obtained from all 3 preparations in which pinna reorientations were carried out.

IPD values are also affected by the angle of elevation of the sound source. Fig.7.3 shows IPD functions at 4kHz for 3 angles of elevation. IPD values decrease progressively as the angle of elevation of the the sound source is increased. At 60° elevation, the IPD function is less asymmetrical about the interaural axis. Rapid phase shifts occurred at some angles of incidence during the collection of the latter set of data. This disallowed of accurate phase meter readings at these angles (e.g. 80°, 90° and 100° azimuth at +30° elevation).

The interaural distance (tragus-tragus) of rabbit MG16 was estimated to be 5.6cm. (The tragus-tragus distance in the rabbit varies with the orientation of the pinnae.) For

Figure 7.1: IPD's at 0° elevation plotted as functions of azimuth for:

e_____e 2.0kHz.

x--------x 3.0kHz.

o.....o 4.0kHz.

(Rabbit MG16, pinna facing 38° azimuth).

Figure 7.2: IPD's at 0° elevation plotted as functions of azimuth at 2kHz:

x_____x pinna facing 132° azimuth.

o--------o pinna facing 38° azimuth.

(Rabbit MG16).

Fig. 7.1

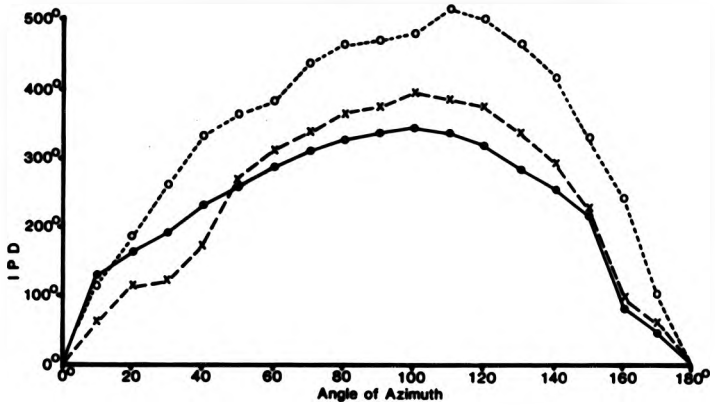
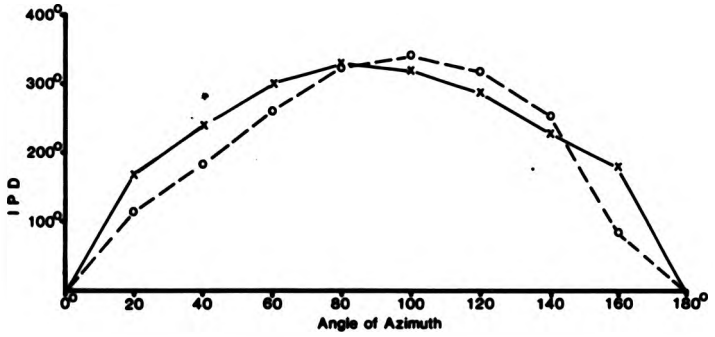

500
400
300
200
100
0
IPD
0
20
40
60
80
100
120
140
160
180
Angle of Azimuth

Fig. 7.2


400
300
200
100
IPD
0
20
40
60
80
100
120
140
160
180
Angle of Azimuth

Ka < 1, where K is the wave number ($2\pi/\lambda$) and a is the radius, the phase derived time differences on the two sides of a sphere are approximately = (3a/c)Sinθinc, where c is the ambient speed of sound and θinc is the angle of incidence of the sound (see Kuhn (1987)). For a sphere of radius 2.8cm, Ka = 1 for λ = 17.59cm. This equates to 1996Hz. The maximum time difference (θinc = 90°) on the two sides of a sphere of radius 2.8cm at frequencies below 1996Hz is therefore approximately 0.24ms.

At higher frequencies, (i.e. for Ka > 1) the time differences on the two sides of a sphere tend to approximate to (2a/c)Sinθinc. For a sphere of radius 2.8cm the time difference for θinc = 90° should approximate to 0.16ms.

The maximum phase derived interaural time differences (ITDp's) calculated from the IPD's for rabbit MG16 are as follows:

2kHz, 0.47ms; 3kHz, 0.36ms; 4kHz, 0.35ms.

The maximum ITDp's obtained experimentally for the rabbit are thus considerably in excess of the maximum time differences on the two sides of a sphere of the same diameter.

7.3. The Rat.

IPD's obtained from Rat Probe 6 at 0° elevation are shown plotted as functions of azimuth in Fig.7.4. The recorded pinna for this preparation was facing 48° azimuth. Up to

Figure 7.3: IPD's plotted as functions of azimuth at 4kHz at various elevations:

e_____e 0° elevation,

x--------x +30° elevation,

o........o +60° elevation.

(Rabbit MG17, pinna facing 30° azimuth).

Figure 7.4: IPD's at 0° elevation plotted as functions of azimuth for various frequencies. (Rat Probe 6, pinna facing 48° azimuth).

Fig. 7.3

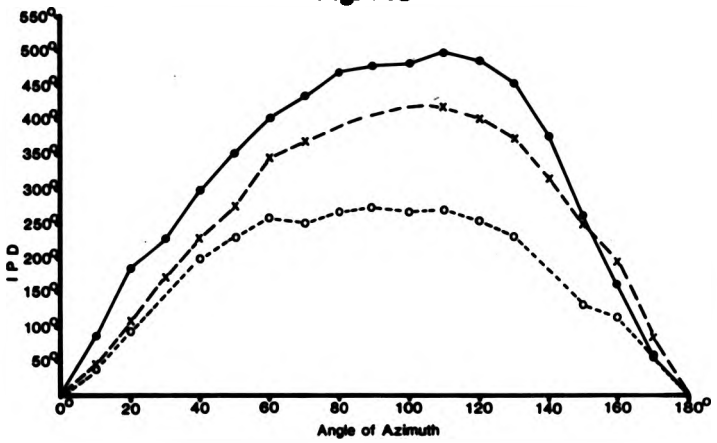
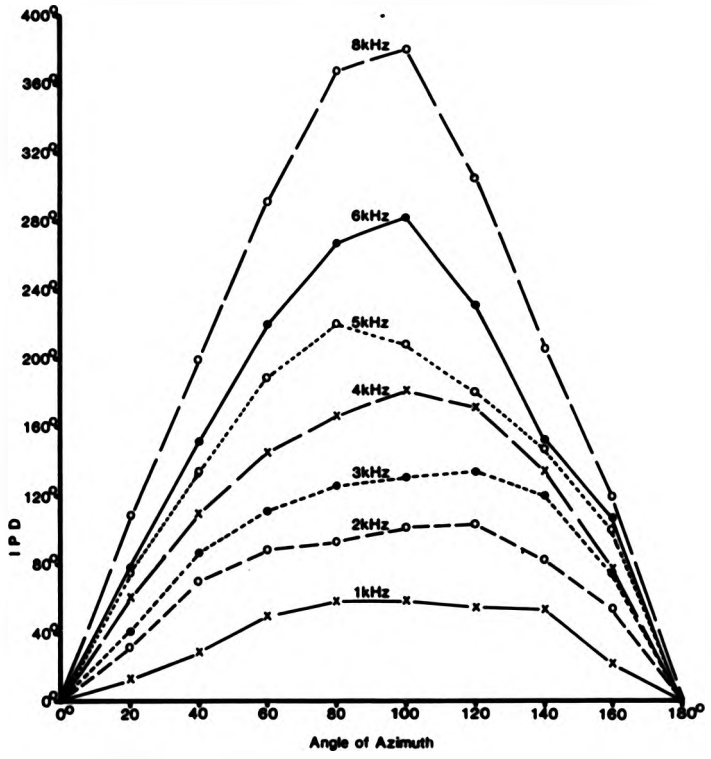

IPD
Angle of Azimuth

Fig. 7.4


8kHz
6kHz
5kHz
4kHz
3kHz
2kHz
1kHz
IPD
Angle of Azimuth

4kHz the gradients of the functions are greater in the posterolateral sector, but at 5kHz and above, they tend to symmetry about the interaural axis. IPD values increase progressively with increasing frequency at all angles of azimuth.

The interaural distance (tragus-tragus) of this specimen was 1.5cm. For a sphere of radius 0.75cm, "ITDp" = (3a/c)Sinθinc = 0.06ms for θinc=90° at frequencies below 7303Hz. The maximum ITDp's for Rat Probe 6 are as follows:

1kHz, 0.16ms; 2kHz, 0.13ms; 3kHz, 0.12ms;
4kHz, 0.13ms; 5kHz, 0.12ms; 6kHz, 0.13ms;
8kHz, 0.13ms.

The maximum ITDp's obtained experimentally are thus double or more the maximum "ITDp's" for a sphere of the same diameter.

7.4. <u>The Guinea Pig.</u>

IPD's obtained from GPC at 0° elevation are shown plotted as functions of azimuth in Fig.7.5. IPD values increase progressively with increasing frequency at most angles of azimuth. The functions do not, in the main, show the steeper gradients in the posterolateral sector that characterise IPD functions obtained from the rat and rabbit. The recorded pinna of GPC was facing 50° azimuth.

The interaural distance of this specimen (tragus-tragus) was 3.0cm. For a sphere of radius 1.5cm, ITDp= (3a/c)Sinθinc = 0.13ms for θinc=90° at frequencies below 3440Hz. The maximum ITDp's for GPC are as follows:

1kHz, 0.19ms; 2kHz, 0.13ms; 3kHz, 0.11ms;
4kHz, 0.13ms; 5kHz, 0.11ms.

The maximum ITDp's obtained from GPC exceed the maximum "ITDp" for a sphere of the same diameter at 1kHz but are equal to or less than this at 2kHz and 3kHz. At frequencies above 3440Hz, the "ITDp's" for a sphere will approach (2a/c)Sinθinc. For a sphere of radius 1.5cm, the maximum "ITDp" will approach 0.09msec at "higher frequencies". Maximum ITDp's for GPC at 4kHz and 5kHz are larger than this.

7.5. Interspecies Comparisons.

ITDp's plotted as functions of azimuth at 4kHz are shown for the 3 species in Fig.7.6. The rabbit, as might be expected from the greater size of its head and pinnae, has considerably larger ITDp's than the guinea pig and rat. The latter 2 species show similar size ITDp's despite the fact that the interaural distance of GPC (3.0cm) was twice that of Rat Probe 6 (1.5cm). This finding may be explained by the differences in the pinnae of the 2 species; the pinna flange of the guinea pig is relatively flat, while that of the rat is strongly curved in cross section.

ITDp's in the rat and rabbit are considerably larger than would be predicted from their interaural distances assuming spherical heads. ITDp's in the guinea pig, however, substantially exceed predicted values only at 1kHz. The head of the guinea pig is not substantially different in shape from that of the rat or rabbit. Greater differences

Figure 7.5: IPD's at 0° elevation plotted as functions of azimuth for various frequencies. (Guinea Pig Probe C (GPC), pinna facing 50° azimuth.)

Figure 7.6: Phase derived ITD's (ITDp's) at 4kHz at 0° elevation plotted as functions of azimuth for:

x_____x rabbit MG16 (pinna facing 38° az.)

•_____• rat probe 6 (pinna facing 48° az.)

o--------o guinea pig C (pinna facing 50° az.)

Fig. 7.5

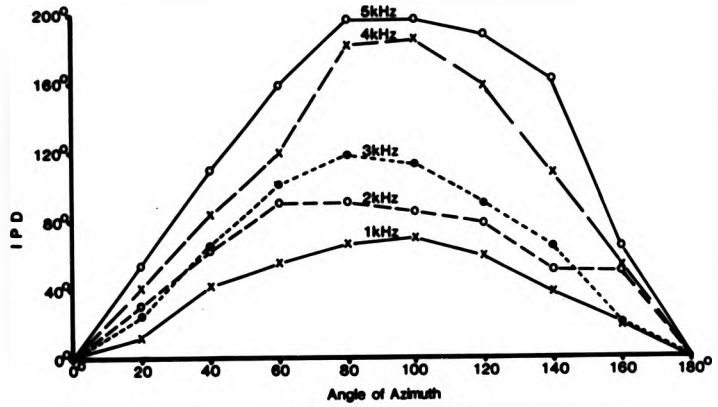
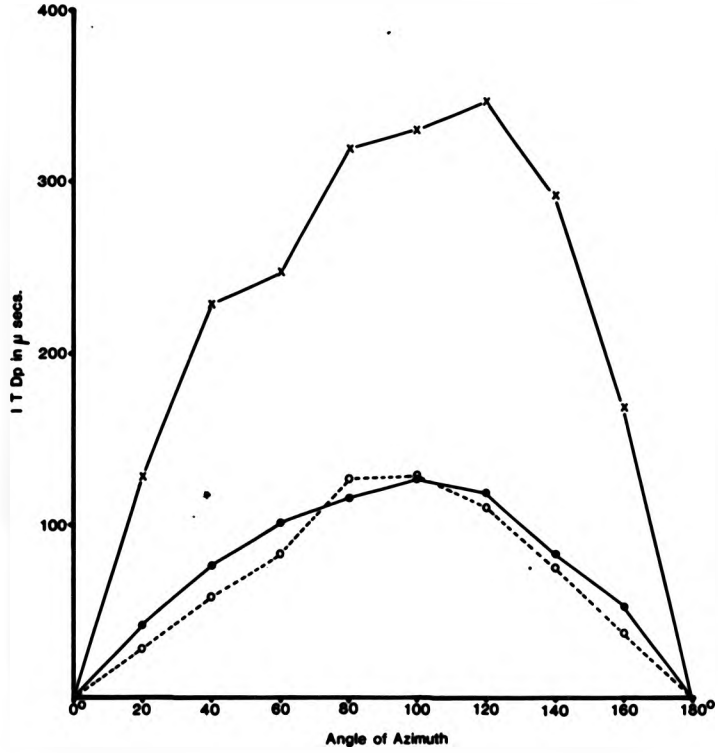

5kHz
4kHz
3kHz
2kHz
1kHz
I P D
200
160
120
80
40
0
0
20
40
60
80
100
120
140
160
180
Angle of Azimuth

Fig. 7.6


I T Dp in μ secs.
400
300
200
100
0
20
40
60
80
100
120
140
160
180
Angle of Azimuth

obtain between the pinnae of these species, and since pinna reorientation in the rabbit results in changes in IPD values, the pinnae must be suspected of being major contributors to ITDp's in at least the rabbit, and perhaps also the rat.

IPD's in the rabbit and rat tend to show steeper gradients in the posterolateral sector. This appears to be related to the anterolateral orientation of the pinnae. A consequence of this is that phase derived directional acuity is likely to be greater when the pinnae are not orientated directly at the sound source.

CHAPTER 8. DISCUSSION.

8.1. Head Related Transfer Functions.

Investigations on the rabbit external ear (chapter 3) provided information on both the efficacy of the different techniques used and the extent of inter-individual variation. The most satisfactory technique (probe implantation in the base of the meatus) was then used to investigate the rat and guinea pig external ears. Inter-individual variation has not been investigated extensively in the latter 2 species. Instead, experiments concentrated on the contributions made by the various parts of the external ear to the HRTF's.

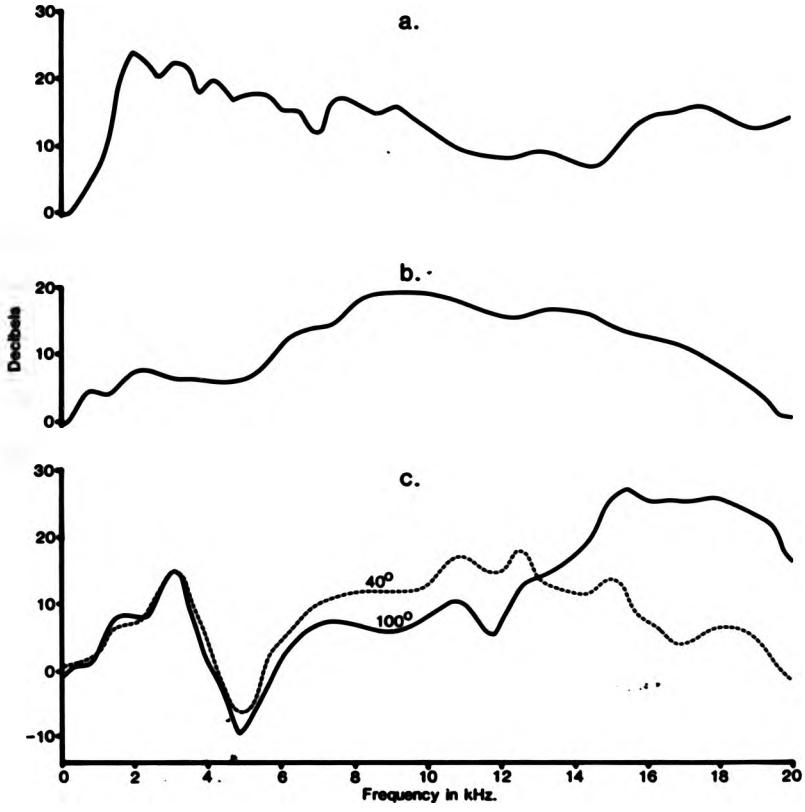
The 3 species show considerable differences in their HRTF's. On-axis HRTF's for the 3 species are shown in Fig.8.1. The rabbit shows the greatest on-axis gain (about 26dB) at lower frequencies (around 2kHz), but the guinea pig shows the greatest gain at higher frequencies (26dB-28dB at between 15kHz and 18kHz). The rat on-axis HRTF shows slightly lower levels of gain in the 50Hz-20kHz range; maximal gain of about 20dB occurs at around 8kHz, but there is substantial gain over an extensive range above this frequency.

Sinyor (1971) reported on the HRTF's of the guinea pig: up to about 12kHz, there is generally good agreement with the present findings. Sinyor did not, however, monitor frequencies above 15kHz and did not report the large gains shown at the higher frequencies.

On-axis gain of the rabbit external ear is largely the

Figure 8.1: HRTF's at 0° elevation from,
(a) Rabbit Probe 9, HRTF at 60° azimuth, pinna facing 25° azimuth.
(b) Rat Probe A, HRTF at 80° azimuth, pinna facing 60° azimuth.
(c) Guinea Pig Probe A, HRTF's at 40° and 100° azimuth, pinna facing 55° azimuth.

Fig. 8.1


a.
b.
c.
Decibels
30
20
10
0
-10
40°
100°
0
2
4
6
8
10
12
14
16
18
20
Frequency in kHz.

result of the effects of the concha on the sound field. The ear canal appears to contribute little to the overall gain, pinna-removed functions (see Fig.4.2(a)) often showing no appreciable gain in the 50Hz-20kHz range. Experiments where HRTF's were obtained under meatus blocked conditions typically resulted in HRTF's of reduced gain (see Fig.4.5). Loss of ear canal gain is a possible cause of this, but protrusion of the plasticene block into the effective concha volume may be contributory. Removal of the top 5cm of the pinna also had little effect on the on-axis HRTF's (see Fig.4.3(a)), but removal of 6cm or more resulted in substantial loss of gain accompanied by an up-frequency shift of the low frequency HRTF peak (see Fig.4.4). This indicates that there may be a standing wave resonance associated with the concha. Removal of the anterior pinna fold resulted in small on-axis losses over an extensive frequency range (see Fig.4.13); the anterior pinna fold clearly contributes to on-axis gain.

The on-axis gain of the rat external ear is the result of the combined effects of the pinna flange and concha. The ear canal appears to make little contribution; pinna removed HRTF's showing only small levels of gain ipsilaterally (possibly explained by head and platform "baffle" effects) and no appreciable gains over most of the 50Hz-20kHz range contralaterally (see Fig.5.19). Removal of the pinna flange resulted in loss of gain throughout the 50Hz-20kHz range, losses tending to increase with

increasing frequency (see Fig.5.18). Pinna flange-removed HRTF's were characterised by a strong, consistent maximum in the 8kHz region. The depth of the rat concha is typically 7mm, and the mean diameter of the concha at the top of the tragal notch is 7mm-8mm. The "expected" axial 1/4 wavelength resonance is in the 9kHz region but further end corrections due to the anterior pinna flange and other parts of the pinna may be appropriate. The 8kHz maximum may therefore be the result of resonance in the concha.

The on-axis gain of the guinea pig external ear is the result of the combined effects of the ear canal, concha and pinna flange. Pinna-removed HRTF's retain the peak in the 2kHz-3kHz region (Fig.6.22) indicating that this gain is associated with the ear canal. However, the ear canals of the guinea pigs used in the probe implant studies were typically about 6mm in length (mouth to TM) and about 3.75mm diameter at the mouth. The "expected" 1/4 wavelength resonance is therefore about 12kHz. Puncturing the TM does not abolish the low frequency peak (Fig.6.23), whereas filling the bulla with water (Sinyor (1971)) does. Sinyor (1971) has suggested that the guinea pig TM and ear canal may show similar acoustic impedances, in which case the ear canal and middle ear cavity may be acoustically coupled at some frequencies.

Removal of the pinna flange in the guinea pig resulted in on-axis HRTF losses at most frequencies above about 4kHz (see Fig.6.21) particularly in the 5kHz-8kHz and 14kHz-20kHz regions, but quantification of these changes

has proved difficult because of preparation instability. Sinyor (1971) reported that pinna flange gain is largest at about 5kHz, but, as stated above, Sinyor did not monitor frequencies above 15kHz. Pinna flange-removed HRTF's show consistent maxima in the 8kHz-10kHz region (Fig.6.21) which may be a consequence of a 1/4 wavelength depth resonance of the concha. The guinea pigs used in this study typically showed conchae of about 7.5mm in depth. Assuming a relatively large end correction, on-axis axial resonance would be expected to occur within the 8kHz-10kHz frequency range. Sinyor (1971) reported the gain of the guinea pig concha to be maximal at between 6kHz and 7kHz. This could be because the guinea pigs used by Sinyor were relatively large. The HRTF's obtained with probe implants in the wall of the ear canal were consistently of larger gain in the high frequency regions than HRTF's obtained with probe implants in the tympanic cavity (compare Figs.6.4 and 6.6). It would appear that high frequency gain reduces with close approach of the probe to the TM. One explanation of this is that the tympanic cavity is comparatively voluminous in the guinea pig owing to the large size of the TM. The gain consequent on the acoustic transformation from "mouth" to "throat" of the external ear is therefore greater in the relatively narrow ear canal than in the tympanic cavity. Khanna and Tonndorf (1972) have shown that at higher frequencies, the vibration pattern of the TM breaks up into isolated zones and the manubrium is driven directly. This may also be the case for the human TM (Tonndorf and Khanna

(1972)). Assuming that this occurs in the TM's of other species, animals with small TM's (such as the rat) would be advantaged in that HRTF gain at higher frequencies would be large as a consequence of the large "mouth" to "throat" ratio; the smaller the TM, the greater this ratio. The large TM of the guinea pig is, therefore, presumably, an adaptation for low frequency sensitivity.

Audiograms obtained for the 3 species show varying degrees of agreement with the on-axis HRTF's. The rabbit is reported to show behavioural threshold minima at 2kHz and 16kHz (Heffner and Masterton (1980)). This agrees well with the on-axis HRTF's which show maxima in the 2kHz region and typically show high levels of gain in the 16kHz region (see e.g. Figs.3.8(b), 3.10, 3.11.). The albino rat is reported to show behavioural threshold minima at 8kHz and 38kHz (Kelly and Masterton (1977)). HRTF's for this species tend to be maximal at around 8kHz (see Fig.5.5) but no comment can be made regarding the 38kHz region because of the restricted frequency range of the probe implant preparations. The guinea pig is reported to show behavioural threshold minima at 8kHz with a second minimum at 1kHz in some individuals (Heffner, Heffner and Masterton (1971)). High gains occur at 8kHz in guinea pig HRTF's (see Figs.6.4 and 6.6) but gains tend to be maximal at around 16kHz. This, however, is only the case for lateral and posterior-ipsilateral HRTF's. Heffner et al. did not test their animals with the sound source positioned at the rear. Low frequency HRTF gains tend to be greatest between 2kHz

and 3kHz and all probe implant preparations showed HRTF peaks in this frequency region. Only one CM preparation showed an obvious low frequency peak, however (see Fig.6.10). It is possible that individual variation accounts for these discrepancies but other factors producing the difference between probe implant results and CM and behavioural findings cannot be ruled out, or identified at this time.

The on-axis HRTF of the cat appears to be the result of gain associated with an axial resonance of the ear canal at between 4kHz and 6kHz and gain associated with the pinna which is maximal at 5kHz. HRTF gain is maximal at about 4kHz (Weiner et al. (1966)). Calford and Pettigrew (1984), however, suggest that the maximum in the 4kHz region is the result of pinna resonance. They suggest that the primary resonance of the pinna occurs at a wavelength equal to twice the depth of the pinna (taken to be 5cm). This suggestion is in error because the cat pinna (as in other mammals) is a cavity terminated by a high acoustic impedance. Axial resonance should therefore occur at wavelengths equal to 4 x the depth of the pinna (+ end correction). Calford and Pettigrew also omitted to include any end correction in their calculation.

The on-axis HRTF of the Tammar wallaby appears to result from a combination of gain in the 4kHz to 8kHz region apparently associated with the ear canal, and gain associated with the horn-like pinna (Coles and Guppy (1986)). The ear canal of the Tamar wallaby is about 1.6cm

in length and the 1/4 wavelength resonance would be expected to occur at about 5.5kHz. It may well be, therefore, that an axial resonance is associated with the ear canal, although other potential sources of pinna-removed gain (such as head "baffle" effects) were apparently not investigated by Coles and Guppy. Resonance associated with the pinna appears to be small or absent in the Tammar wallaby; experimental enlargement of the pinna did not result in any discernible down-frequency shift of HRTF features. Coles and Guppy showed that the gain function of the pinna approximated to the gain curve of a finite-length conical horn.

On-axis pinna gain functions of 2 species of gleaning bats were also shown to approximate to the gain curves of finite-length conical horns (Guppy and Coles (1988)). The larger of the 2 species (Macroderma gigas) was also reported to show a meatus associated resonance, but since the TM was replaced by the microphone, it is not possible to predict whether or not resonance would occur in a normal meatus.

There thus appears to be considerable variability in the acoustical properties of the external ears of the mammals investigated to date. The ear canals of species such as the guinea pig, cat, human (Weiner and Ross (1946)) and perhaps the Tammar wallaby contribute to HRTF gain as a consequence of their resonant properties. Canal resonance appears to be small or absent in the rabbit and rat, and also in the Australian gleaning bat, Nyctophilus gouldi (Guppy and

Coles (1988)). The pinnae of the rabbit, human (Yamaguchi and Sushi (1956)) and perhaps the cat (Weiner et al. (1966)), rat and guinea pig, exhibit axial resonance whereas the pinnae of the Tammar wallaby and 2 species of gleaning bats do not.

8.2. Azimuthal Directional Characteristics.

Up to certain frequencies, the azimuthal dependence functions, obtained from the three species under investigation, all show relatively smooth, rounded, main lobes with indications of a "bright spot" contralaterally (see Figs.3.2, 5.2, 6.2.). This type of azimuthal dependence function obtains up to about 5kHz in the rabbit, 20kHz in the rat and 10kHz in the guinea pig. In the human (Shaw (1974a)) azimuthal dependence functions up to 1000Hz are similar to those obtained from a sphere of the same dimensions as the head. "Head effects" are the main determinant of horizontal directivity up to 2.5kHz in the human but at frequencies above 2.5kHz, the main lobes of the azimuthal dependence functions in the human become noticeably "sharper" because at, and above this frequency, the effects of the pinna on the sound field are large (Kuhn (1987)). Experiments on the rabbit, where the effects of pinna reorientation and removal have been investigated, show, however, that at 2.0kHz, the major determiner of horizontal directionality in this species is the pinna (see Figs.3.4 and 3.5). This is not surprising, in that the pinna mouth of the rabbit is above the level of the head.

This is also the case in the rat and, to some extent, in the guinea pig. The head diameters of the latter 2 species are in the region of 3cm and 4cm respectively. Large "head effects" would therefore not be expected below about 11kHz and 8.5kHz, even for sound source positions below 0° elevation when the head does become interposed between the pinna openings. In the rabbit, rat and guinea pig, the pinnae rather than the head, are likely to be the major determiners of horizontal directionality.

Over the frequency ranges investigated, assessment of horizontal directionality in terms of -3dB acceptance angles shows the rabbit pinna to be the most directionally sensitive of the 3 species, with acceptance angles of between 20° and 40° azimuth at 8kHz and above in the most sensitive preparations (see Fig.3.3). This is a similar level of directionality to that reported by Coles and Guppy (1986) for the Tammar Wallaby. The guinea pig shows gradually decreasing acceptance angles with increasing frequency, acceptance angles dropping to 40° azimuth at 20kHz (see Fig.6.3). The rat appears to be the least directionally sensitive of the 3 species in the 50Hz-20kHz range, -3dB acceptance angles generally being no better than 60° azimuth at 20kHz (see Fig.5.3).

HRTF families obtained from the 3 species support and extend the pure tone data discussed above. In the rabbit, HRTF's at 0° elevation tend to show increasing separation from about 4kHz but there are regions above this frequency in each preparation where HRTF separation is poor and often

non-progressive (see e.g. Fig.3.6). In the rat, HRTF's show consistent but relatively small degrees of separation above 12kHz in 3 of the 5 probe implant studies (see Figs.5.4 and 5.5). In the guinea pig, best overall separation is shown in the posterior-ipsilateral HRTF's. Progression and clear separation of the spectra in this sector occur both in the 6kHz to 10kHz and in the 16kHz to 20kHz regions, whereas separation and progression of HRTF's in the anterior-ipsilateral sector are not clear-cut (see Figs.6.4 and 6.6).

CM spectra obtained from the 3 species generally confirm the findings of the probe implant studies (see Figs.3.18, 3.20, 5.9, 5.10, 6.9, 6.10). In the rat, the ipsilateral CM spectra show clear separation well beyond 20kHz indicating that directional sensitivity in the rat extends into, and is perhaps best at, frequencies above 20kHz.

In the guinea pig and, to a lesser extent, the rat, the pinna can be subdivided into concha and pinna flange, the fossa comprising a distinct pocket within the pinna flange (see Figs.5.1 and 6.1). In the rabbit, there is no clear demarcation between concha and pinna flange, and the fossa is contained within the concha volume below the level of the tragal notch (see Fig 4.1). Detailed investigations into the contribution of the pinna flange to the directional characteristics of the external ear have therefore been carried out on the rat and guinea pig only. In both of the latter 2 species, pinna flange removal results in decreases in gain ipsilaterally and increases in

gain anteriorly (see Figs.5.18 and 6.21). The increases in gain occur at high frequencies whereas decreases in gain occur over a wide frequency range. The obvious interpretation of these findings is that the pinna flange contributes to on-axis gain while the recurved leading edge of the pinna serves to "shadow" high frequency sound from the anterior sector. In the guinea pig, the anterior pinna fold and fossa form a distinct region of the pinna flange. Removal of this region also results in high frequency gains in the anterior sector (see Fig.6.20). It is also clear that in the guinea pig, the anterior part of the pinna flange contributes to the large high frequency gains from the posterior sector (see Fig.6.20).

The fossa of the rabbit and guinea pig external ears forms a distinct pocket. Blocking the fossa resulted in frequency shifts in HRTF nulls in both species but only in the 0° azimuth HRTF's of the guinea pig were these shifts consistent and of significant proportions (see Figs.4.26 and 6.18). The down-frequency shift of the guinea pig HRTF nulls appears to be associated with loss of gain in the 11kHz region (there are some losses in this frequency region in the 120° azimuth HRTF of GPC). This finding appears to partially contradict the findings of the anterior pinna fold-removal experiments. The 2 experiments are not corollaries, however, as the anterior pinna fold is retained in the fossa-blocked preparations. The tentative conclusion to be drawn from this is that, in the guinea pig, the fossa generates gain in the 13kHz region.

particularly at 0° azimuth, but that anterior pinna fold "shadow" reduces gain from the anterior sector at higher frequencies. Anterior pinna fold removal was also carried out on the rabbit (see Fig.4.13) with considerable effects (largely losses) over a range of frequencies. The anterior pinna fold of the rabbit is, however, an "inner lip" on the recurved leading edge of the pinna (see Fig.4.1) and is not equatable to the structures of the same name in the rat and guinea pig.

Butler and Flannery (1980) report that monaural human subjects appear to have "maps of spatial referents" (SRM's) based on stimulus frequency. Butler (1987) reports that individual HRTF's and SRM's matched; the angle of azimuth at which a particular frequency peaked in the HRTF was the perceived location when bands of that centre frequency were broadcast. SRM's appear to be used by humans to enhance auditory acuity in the lateral sectors where binaural cues are relatively weak (Musicant and Butler (1985)). There is little indication of progressive shifts in HRTF or azimuth dependence function peaks with angle of azimuth in any of the 3 species investigated here.

8.3. Elevational Directional Characteristics.

Progressive increases in HRTF gain with increases in elevation occur in all 3 species. These increases tend to be confined to particular frequency regions in each species and are clearest in ipsilateral HRTF's. In the rabbit, these changes typically occur in the 4kHz-8kHz range (see

e.g. Fig.3.7). In the rat, these changes occur in the frequency range above 12kHz (see Fig.5.6) and in the guinea pig in the 9kHz-13kHz range (see Figs.6.5 and 6.7). These findings are generally substantiated by CM studies. In the rabbit, however, only some CM preparations showed these effects (see Fig.3.21), other preparations showing non-progression of CM amplitude with increasing elevation (see Fig.3.19(a) and (b)). The CM interference phenomenon may be responsible for this. In the rat, progressive changes in CM amplitude with increasing elevation occurred at both ipsilateral and contralateral angles of azimuth (see Fig.5.11), but the contralateral effects occurred at lower frequencies. In the guinea pig, the CM studies indicate that the effects are limited to ipsilateral angles of azimuth and are apparently confined to a relatively small frequency range (see Figs.6.11 and 6.12).

Blocking the fossa in the rabbit and guinea pig appears to have little effect on the progressive HRTF changes with elevation. In the rabbit, fossa blocking causes only small, variable effects, and in the guinea pig the effects are largely limited to the HRTF's at 0° and 120° azimuth (see Fig.6.18). Furthermore, HRTF's at various angles of elevation at 0° azimuth (Fig.6.19) show progressive changes with elevation under fossa-blocked conditions, although gain is reduced in the 13kHz region. The fossa does not, therefore, appear to be the primary cause of the elevation effect.

In the rabbit and guinea pig, where HRTF nulls occur,

they tend to show progressive up-frequency shifts with increasing elevation of the sound source (see e.g. Figs.3.7 and 6.7(a)). Kuhn (1987) reports that the likely cause of on-axis HRTF nulls in the human is destructive interference between reflected and incident sound waves at the entrance to the ear canal. The reflections are from the curved internal surface of the concha, and since the opening of the ear canal is asymmetrically positioned within the concha, the reflected sound will be 180° out of phase with the incident sound at different frequencies for different sound source positions. In particular, the higher the elevation of the sound source, the higher the frequency at which the out-of-phase relationship will occur. The similarity between the human and guinea pig external ear would suggest a similar cause of HRTF nulls in the guinea pig. The modelling experiment described in chapter 4.9 indicates that interaction between incident sound and sound reflected from the "pinna" face may also be the cause of the on-axis HRTF nulls in the rabbit (see Chapter 4.9). Where destructive interference occurs, it might be expected that constructive interference may also occur. In irregular structures such as the mammalian pinna, it is not possible to predict the frequencies at which the constructive interference would occur, but it seems likely that the increase in HRTF gain with increased elevation shown by the 3 species under investigation is, at least partially, the result of constructive interference. Guppy and Coles (1988) have described the external ears of 2 species of gleaning

bats as obliquely truncated conical horns. The elevation-dependent axis shifts of the ears have been explained in terms of interaction between the sound travelling along the long and short sides of the horn. Reflections from the pinna face have not been specifically included in this explanation and it is therefore likely to be an oversimplification.

Acoustic axis shifts of the external ear with increasing frequency have been reported for the Tamar wallaby (Coles and Guppy (1986)), for 2 species of gleaning bats (Guppy and Coles, (1988)) and, to a small extent, for the cat (Phillips et al. (1982)), although, in the latter study, abnormal positioning of the recorded pinna may have been the cause (Calford and Pettigrew (1984)). The up-frequency shifts of HRTF features with increasing elevation reported for the 3 species under investigation here would also result in axis shifts with frequency. However, concentrating on the acoustic axis, as such, would obscure the range of the effects. Only when HRTF series are examined in detail do the range and consistency of the elevation effects become clear. It may therefore be that the elevation effects found in the rabbit, rat and guinea pig are a common characteristic of the mammalian external ear.

8.4. Interaural Intensity Differences.

Clements and Kelly (1978) and Judge and Kelly (1981) report that in guinea pigs and rats respectively, monaural blocking prevents effective auditory localisation. The primary cues for localisation are therefore considered to be binaural. Large, progressive changes in IID with angle of azimuth occur in all 3 species investigated here. This is evident from IID spectrum families (Figs.3.22, 3.23, 3.24, 3.25, 3.27, 5.12, 5.13, 5.14, 6.13 and 6.14), and from IID's at various frequencies plotted as functions of azimuth (Figs.3.29, 3.30, 5.17 and 6.17). All 3 species show largest rates of change in IID in the anterior sector, and a tendency to show erratic changes with angle of azimuth in the posterior sector. The anterior pinna flange has been shown to be contributory to the "shadowing" of high frequencies from the anterior in the guinea pig and perhaps also in the rat. This is the likely case in the rabbit also, since the leading edge of the pinna is strongly recurved (see Fig.4.1). The pinnae of the 3 species all tend to face anterolaterally and auditory acuity, with the possible exception of the guinea pig in the 16kHz region, is therefore highest in the anterolateral sector. The anterior pinna flange is therefore necessary for the establishment of progressive changes in gain that confer the large, progressive changes in IID in the anterior sector. Since the pinna opening extends below the dorsal surface of the head in the guinea pig the head may

also contribute to azimuthal plane IID's at some frequencies in this species.

In the rabbit, IID spectra typically show a series of peaks (see Fig.3.22) which are the result of contralateral nulls. The sizes of the peaks depend on the signal : noise ratio of the ear and recording system. It is therefore clear that the largest IID's available to the rabbit cannot be independent of signal level. The contralateral nulls also result in rapid changes in IID with frequency (see Fig.3.29).

In the rat, IID's also vary with frequency, but there is a general trend towards increasing value with increasing frequency, the largest values occurring at the highest frequency (20kHz) at which reliable recordings could be made. The rat IID functions obtained in this study show some measure of agreement with those obtained by Harrison and Downey (1970), although the functions obtained by the latter were more erratic and, at 20kHz, substantially smaller. Differences in probe performance and placement may account for these differences.

Kelly and Glazier (1978) report that the rat shows a mean localisation threshold of approximately 28° azimuth. Rat IID's obtained in this study change at the rate of up to 0.3dB per 1° azimuth. If IID's are used to assess the angle of azimuth, this would apparently indicate a JND of up to 8.4dB. This is remarkably large, and indicates that either the results of behavioural testing in humans and species such as the rat are not directly comparable or that IID's

are not being used by the rat to assess angle of azimuth in the way that is generally supposed. This is discussed further below.

In the guinea pig, there are 2 distinct frequency regions where large, progressive IID's occur; in e.g. GPA, these are the 4kHz-10kHz and 16kHz-20kHz regions (see Fig.6.13). Much of the gain in the higher of the 2 frequency regions is associated with the anterior pinna flange, and directionality is largely conferred by the anterior pinna fold. Gain in the lower frequency region is associated with the concha and pinna flange and directionality is presumably conferred by the orientation of the pinna as a whole.

IID's plotted as functions of azimuth tend to show steeper and more uniform gradients in the anterior sector in a variety of species of mammals. This has been shown to be the case in the human (Shaw (1974a)), the cat (Moore and Irvine (1979)) and the species investigated by Harrison and Downey (1970) (squirrel monkey, rat, a bat species and humans). The rabbit and guinea pig may now be added to this list, indicating a general tendency among the mammals for greater potential IID-based directional acuity in the anterior sector of the azimuthal plane.

IID spectrum features show progressive up-frequency shifts with elevation in all 3 species investigated. These shifts occur at all angles of azimuth not on the mid-sagittal plane. The shifts tend to be greatest in the region of the azimuthal plane and to cease at high and low

angles of elevation. In the rabbit, the spectra obtained from any one angle of elevation have a characteristic appearance conferred by the frequency position of maxima and minima (see Figs.3.24 and 3.26). In the rat, the frequency position of the maximum in the 16kHz-27kHz is determined by elevation (see Figs.5.15 and 5.16). In the guinea pig, the minimum in the 12kHz-14kHz region (Fig.6.15) and the maximum in the 20kHz-24kHz region (Fig.6.16) show progressive shifts over a range of elevations. The physical causes of the IID spectrum feature shifts appear to be the progressive changes with elevation in HRTF features (discussed above); the changes occur at higher frequencies ipsilaterally than contralaterally (see Fig.5.11).

8.5. Interaural Time Differences.

All 3 species under investigation show progressive changes in phase derived ITD's (ITDp's) with angle of azimuth. In the rabbit and rat, the gradients of ITDp's plotted as functions of azimuth are steeper in the posterior sector (see Fig.7.6), probably because of the anterolateral orientation of the pinna. This supposition is based on the finding that pinna reorientation in the rabbit results in changes in shape of IPD functions (see Fig.7.2).

Low frequency derived maximum ITDp values for the 3 species are considerably larger than those predicted from spheres of the same diameter as the animals' heads, but ITDp's in the guinea pig are of similar values to those of

the rat, despite the smaller head size of the latter. The shallower pinnae of the guinea pig may explain both this, and the finding that IPD functions in the guinea pig are relatively symmetrical about the interaural axis at a number of frequencies (see Fig.7.5).

ITD's measured on the cat head (Roth et al. (1980)) also reveal that the "acoustically effective head size" is greater than predicted from actual head size. Roth et al. also showed that retracting the pinnae resulted in reduced ITD values. Above Ka=1, ITD values decrease with increasing frequency in the rabbit, rat and guinea pig. This was also shown to occur in the cat by Roth et al.

Kelly (1974) reports that the limit of discriminability of time intervals between paired clicks in albino rats was approached at time differences of between 62us and 31us. The rate of change of ITDp in the anterior sector (0°-60° azimuth) at 1kHz is 23us per 10° (calculated from Fig.7.4). The rat should therefore be able to discriminate between sound sources separated by between 13° and 27° azimuth at this frequency. Kelly and Glazier (1978) report that the mean localisation threshold of the albino rat to click trains is approximately 28°. Maa's for the wild Norway rat are reported as being between 11° and 13.5° for 100ms bursts of broad-band noise and between 12.5° and 15° for clicks. There appears to be some degree of agreement between the behavioural and biophysical findings. It should, of course, be remembered that localisation of pure tones is considerably poorer than for broad-band sound in

all mammals where this has been investigated. The possible reasons for this are discussed below.

Masterton et al. (1969), in a discussion of the evolution of human hearing, report a strong correlation between the interaural distance and the upper frequency limit of hearing in mammals. Small-headed mammals are supposedly disadvantaged by smaller rates of change in ITD in the azimuthal plane. Directional sensitivity based on IID's is supposedly greater at high frequencies, and high frequency hearing therefore "compensates" for poor ITD sensitivity. It is now clear that the role of the pinna in determining both ITD's and IID's must be taken into account; pinna effects cannot be predicted from a species' interaural distance. The present findings show this clearly.

8.6. General Considerations.

The external ears of the rabbit, rat and guinea pig are not scale versions of each other. The depth of the concha, size and position of the fossa, the shape of the pinna flange and the size of the TM are quite different in the 3 species. This is reflected in the on-axis HRTF's which show not only maxima at different frequencies, but different distributions of minima and covert maxima. The rabbit ear appears to be adapted to give maximum gain at about 2kHz and achieves this by means of a comparatively deep concha. An animal of similar size to the rabbit is the cat, yet maximum HRTF gain in this species is at 4kHz (Weiner et al.(1966)). Maximum gain in rat HRTF's does not occur until

8kHz or more, but gain then remains high over an extended frequency range. The guinea pig on-axis HRTF shows a peak at between 2kHz and 3kHz despite a relatively small and shallow pinna. The low frequency peak appears to be the result of resonance in the tympanic bulla and ear canal, but the "penalty" for this is the minimum in the 4kHz-6kHz region and less gain at higher frequencies.(Sinyor (1971) reports that the pinna-removed HRTF shows loss of gain over an extended frequency range). Pinna gain compensates, in part, for these effects, but the high frequency "performance" of the ear is, nevertheless, reduced. The large size of the tympanic membrane results in a relatively small mouth to throat ratio of the external ear and at high frequencies, the tympanic membrane is unlikely to transmit all the sound power incident at its surface (Tonndorf and Khanna (1972), Khanna and Tonndorf (1972)). The rabbit and guinea pig thus appear to be adapted for low frequency hearing, while the rat is adapted for acuity over an extended range of higher frequencies.

Detailed reports on the sound localisation abilities of the rabbit and guinea pig appear not to have been published. There are, however, a number of reports on the localisation ability of the rat. Despite the poor low frequency gain of the rat HRTF, the rat is reported to show a bimodal distribution of errors when tested with pure tones, an increased error rate occurring in the 8kHz region (Masterton et al. (1975)). This suggests that the rat uses time cues below 8kHz and intensity cues above 8kHz. The rat

HRTF peaks at around 8kHz, but directional sensitivity of the HRTF families is low in this frequency region. This is a similar situation to that of the human, where the region of maximal HRTF gain (2.5kHz) (Shaw (1974)) is where directional acuity is reduced (Stevens and Newman (1936) and Mills (1958)). High HRTF gain does not therefore necessarily imply high directional acuity.

Much of the research on directional hearing has concentrated on directional acuity in the azimuthal plane. This is true of both biophysical and behavioural work. In many circumstances, however, the localisation task facing an animal may be 3-dimensional. In these circumstances ITD and IID values are of limited use unless the elevation of the sound source is known or "set" in some way. It is, of course, possible that the animal makes an assumption that the source is on e.g. the azimuthal plane, in which case distinguishing front from rear would seem to be the only major problem. For many animals this would seem unlikely however. Arboreal animals and animals such as the rat (the albino rat has been developed from the Norway rat, well known for its climbing ability) would be disadvantaged by such a strategy. It is becoming clear that man and other primates, such as some macaque species (Brown et al. (1982)), can localise sounds in the vertical plane. In man, the cues used appear to be spectral features such as the frequency positions of minima, and perhaps the levels of gain in certain frequency regions (Shaw (1974)). Cues of this nature have been shown to be potentially available to

the 3 species presently under investigation. Spectral minima in the HRTF's of these species have been shown to be sporadic in occurrence, but progressive increases in gain with increasing elevation consistently occur in particular frequency regions. It has also been shown that progressive up-frequency shifts in IID spectrum features occur with increasing elevation. IID cues are not available in the mid-sagittal plane but there appears to be no reason why they should not be used outside this plane.

The anterior pinna folds of the rabbit, rat and guinea pig appear to be adaptations for producing large, progressive changes in gain (and hence in IID's) in the anterior sector of the azimuthal plane. This indicates that cues in the frequency/intensity domain are used to determine the angle of azimuth of incident sound in the anterior sector.

The progressive changes in ITD's in both anterior and posterior sectors of the azimuthal plane are also likely to be useful directional cues. The tendency for ITD's to show larger rates of change in the posterior sector (in the rabbit and rat) may compensate for the erratic nature of posterior sector IID functions.

Resolving front from rear may be accomplished using spectral cues. Blauert (1969) has shown that humans distinguish front from rear by means of spectral cues and Shaw (1974a) has pointed out that clear-cut differences obtain between anterior and posterior sector HRTF's in the human. Anterior and posterior sector HRTF's in the guinea

pig are distinctly different, but this is not the case in the rat and rabbit. In the latter 2 species, however, front/rear resolutions could be made by comparing ITD and IID values. ITD's and IID's plotted as functions of azimuth show asymmetries about the interaural axis, but in opposite directions. ITD functions in the rat and rabbit show a steeper gradient in the posterior sector, while IID functions show a steeper gradient in the anterior sector. The direction or "sign" of the ITD / IID mismatch should therefore be indicative of the azimuthal sector of the sound source.

Behavioural tests of human directional hearing typically involve the positioning of the sound source in one plane only. Subjects are usually aware of this and may well be able to use this information to resolve potential confounding of azimuthal and elevational dependent changes in IID and IPD values. Other species may not be capable of doing this which may, in part, explain the large discrepancies between the localisation performances of humans and other species. This study has shown that IID functions in the rabbit, rat and guinea pig are as directionally sensitive as those of the human. The proper way of conducting inter-species comparisons of directional capabilities may therefore necessitate 3-dimensional tests along the lines of the "sound cage" experiments of workers such as Angell and Fite (1901).

The angle of elevation of the sound source and potential front/rear confusions appear to be resolved by reference to

spectral cues in humans. This is also likely to be the case in other mammalian species, at least for the determination of angle of elevation, and spectral cues have been shown to be available for this task in the 3 species under investigation here. Spectral cues are not available from pure tone signals, and it is therefore not surprising that pure tone sources are not localised as accurately as broad-band sources in the mammals. The indications are, at present, that the mammalian ear is adapted for the 3-dimensional localisation of broad-band signal sources. Spectral cues (both monaural and binaural) are available to "set" angle of elevation, which would then facilitate the use of ITD's and IID's to determine the angle of azimuth with some degree of accuracy.

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